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THE PHYLOGENY OF SEXUALITY AND TRIPHYLETIC EVOLUTION OF THE LANDPLANTS*

With 27 figures and tables

P. GREGUSS

József-Attila University, Szeged, Hungary

Motto:
One must not fear hypotheses, if they are apt of making us able to look through a chaos of facts.

Oltmans

Introduction

All living beings in nature, plants and animals alike, are directed by two fundamental laws of nature, the instincts of self-preservation and of race-preservation. The instinct of self-preservation assures the vegetative life of the individual, while the instinct of race-preservation the survival of the race. This double process is realized in Unicellular organisms by the same individual while in Multicellulars vegetative life is assured by the so-called vegetative cells or organs, and the survival of the race by the sexual, reproductive cells or organs. A single cell or individual is sufficient to provide for vegetative life, whereas sexual propagation invariably requires the fusion of two contrasting, + and —, in the widest interpretation of a male and a female cell.

In the following we propose to investigate the patterns of the sexual reproduction in the vegetable kingdom, and particularly of the plants living in fresh water and on land. These patterns of sexual propagations have been realized in the development of the terrestrial flora during a period of two to four thousand million years, always by a necessary adaptation to environmental conditions of life. We do not propose to extend investigations to the history of developent of the sexual propagation of marine plants this time, because in our opinion the development of terrestrial and fresh water vegetation in the course of 2 to 4 thousand million years intervened independently of the development of see-weeds (GREGUSS, AXELROD). It should be noted, however, that the plants of the seas essentially and by necessity reached the same degree of development as did the phanerogams on land by our days. Here we want to point to the completely similar processes of the alternation of generations which intervened in the infinite course of times parallel to each other and in the same way both in the seas and in fresh waters and on land. (Sea-*Flagellatae,* fresh-water *Flagellatae; Cutleria-Musci; Dictyota-Pteridophyta; Laminaria-Gymnospermae* and *Angiospermae.)*

Similarly we do not dwell on the sexual propagations of *Fungi* and *Lichen* because they generally agree with the reproduction in the fresh-water *Algae;* moreover, the *Fungi*

* The author was reading this paper at the University of Greifswald and Rostock and at the Highschool of Pedagogic Potsdam (in Germany) at the University of Cluj and Bucuresti (Roumanie) and the Hungarian Geological Society and the Hungarian Biological Society, in India Lucknow, Delhi and Bombay.

did not play a decisive role in the development of Cormophytes, at best they lived with them in symbiosis.

In the simplest unicellular fresh-water and land plants of course the sexual act could not have been in the past neither is it at present so complicated and of such high order as among the most developed plants, but the essence is the same both in the unicellular and in the highest terrestrial phanerogams.

To become acquainted with the thousand millions of years old history or philogeny of the sexual propagation of land plants, i. e. of the formation of the different developmental stages of sexuality, investigation must be started right at the beginning, where the first traces of sexuality can be conjectured, to gradually proceed towards ever more developed conditions. Where does the state appear for the first time, where does it begin, in which already the contrast of sexuality, its two forms, the male and female sexes can be suspected to exist?

Contrasts in nature

According to the ancient Greek philosophy, but also according to the philosophy of HEGEL, ENGELS and MARX, there is a constant contrast between objectives and phenomena of nature, and from this constant contrast evolution and progress are born. These contrasts are very frequent not only in inanimate nature but also in the life or organic world and one might even state that this is the general law. We may point in this respect to positive and negative magnetism in physics, to the so-called dipole-systems or to the + and — electricity where the two kinds of energy are of opposite nature, where the electric charges of the same kind repulse while those of different kind attract each other and when they merge, a third phenomenon, e. g. an electric discharge ensues. When, on the other hand, the two are present to an identical degree, there is apparent rest. The essence in both cases is that the same kind of energy has two essentially different features and both are characterized by the repulsion of the same kind and by the attraction of the different kinds or their readiness for fusion respectively.

In chemistry the same law of nature prevails. The compounds are generally acid or alkaline, possibly neutral. Acids and bases have contrasting features and therefore they eagerly unite, producing a new matter, (amphoter) a salt. In the salt there is something of both compounds, still it differs from both of uniting compounds (K_2SO_4). And if in the resulting salt one of the components somewhat prevails over the other then possibly an *acid salt* ($KHSO_4$) or an *alkaline salt* [Ca(OH)Cl] originates. We may also refer to the phenomenon of intersex or of the prevalence of male or female character in the organic world.

There are such contrasts, however, not only between the various compounds, but the same compound may have so called isomeric forms where there arise certain contrasts in the compounds in the mutual relationship of individual elements or groups of elements, in their special configuration; they may be possibly the reflections of each other and all these appear also in the character of the compound. One of the isomeric compounds e. g. turns the plane of the polar light to the right, the other to the left. Among the salts originating from the interaction of acids and bases the metal represents and carries of transfers the + electricity which for instance in electrolysis segregates at the — pole while the acid radical transfers the — electricity segregating at the + pole. Thus also in chemical processes the essential feature is that invariably contrasting forces act and a new compound different from the others is born from the interaction.

It is another well known fact e. g. that the relationship between cis and trans crocetin-dimethylester for instance in the male individuals of *Chlamydomonas eugametos* is 3 to 1 while in the female individuals 1 to 3 and a significant change of this relationship might change the character of the sexuality as well. From this on the other hand it may be inferred that in the living organisms there are similar or may be identical compounds as in the inanimate world so that there is no essential difference between the two spheres in this respect. In the living organisms and generally in the compounds of the living substance the same physical (electricity, magnetism) and chemical processes (replacement reactions) take place as in the inanimate (inorganic) substances. If it is so, however, the idea may be raised, and properly, that perhaps at the origin of organic world, when from the inorganic matters organic compounds and from the latter living substances developed, entirely similar and possibly even identical processes took place as those which we can observe in our in the inorganic and organic world.

Stage I. The origin of living substance

There can be and as a matter of fact is no doubt in our time that the development of the organic world started from the inorganic compounds. But as to how the first steps, the first attempts might have occurred, is widely open to discussion. We do not propose to deal with the various theories on this subject but accept as a postulate the statement that the living matter derives from the inert and his inorganic elements, and anyhow these first attempts took place, the fundamental principle i. e. the contrast between the elements and compounds existed already between the simplest elements and compounds. Electricity and magnetism were active in them from the very beginning and thus the possibility was given from the outset that more complex compounds could develop from the simplest ones, first simple and than more and more complicated organic compounds from the inorganic substances and finally from the inert and thus inorganic elements, and anyhow these first attempts could originate. According to the present state of science and also to individual opinions the most important constituents of this living matter could have been compounds of the nucleic acid type which are full of the most various dipole systems, to mention nothing else than the dipolic arrangement of the water molecules in them. The more complex a compound is, the more and the more various isomers it may possess, and might have possessed in the past, the fundamental principle, the chemical or electrical attraction and repulsion having remained in all of them. All this processes are likely to have taken place in a liquid and warm environment. From the increasingly more and more various isomers of the many kinds of compounds gradually organic matter complexes, so-called coacervates, and from these protoplasm type substances characteristic of the living matter separated, which as viewed at the light of modern science could be regarded already as the beginning of life. In this plasmatic matter gradually a nuclear substance started to form until finally the incredible variety of unicellular living beings developed upon the action of environmental factors. Since these primary cells had also been constituted by compounds and in the compounds, as an ancestral nature of law, the two contrasting effects, attraction and repulsion as well as the principle of fusion continued to exist, so already in the protoplasms separated into the most primitive cells the concequence of the positive and negative separation and fusion respectively existed, which ultimately may be considered already as the most rudimentary manifestation of the two sexes.

Stage II. Virophyta

It must be presumed that this sort of phenomena occur already in the viruses which are at the limit of life, since they also exhibit the + and − character. The *Virophyta* can not be qualified with certainty as living beings or inert matter. Science had established that they have some features suggestive partly of living organisms (propagation) while others point to inanimate matter (minerals). As to their propagation it only takes place in living cells or organisms, without showing, however, the least external mark of sexual reproduction. They show the first manifestation of sexuality in as much as contrasting com-

Stage II. VIROPHYTA

(Fig. 1)

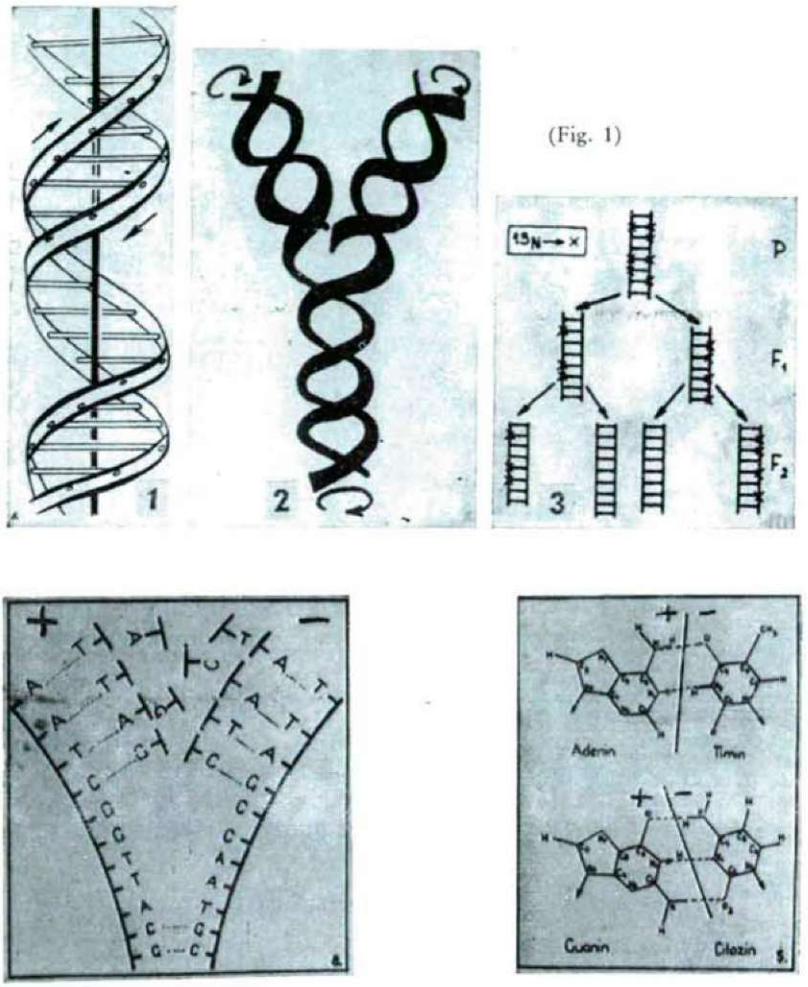


Fig. 1. Simplified WATSON—CRICK model on the structure of the DNA molecule. In the double spiral run the ribose and phosphoric acid radicals while along the perpendicular lines the purin and pyridin rings are arranged which are linked with two hydrogen bonds.

Fig. 2. Schematic illustration of the spiral self-reproduction of DNA.

Fig. 3. The DNA "increase" of the bacterium X marks the place of heavy nitrogens in the DNA of the "parent" (P) bacteria, while F_1 and F_2 designate the "labelling" of DNA originated in the first and second generations.

a) The two threads of the DNA separate and from the basic compounds the complementary thread develops.

b) Hydrogen bonds between the individual purin and pyramidin bases. (CSÁNYI, Természettudományi Közlöny 1962).

pounds, groups of compounds or their isomeric forms may exist in them, since for instance one strain of the same bacteriophage only attacks F—, while its other strain F+ individuals contrasting to the former. This contrast, according to most recent investigations, can be traced back to the chemical composition of DNA. It is known to-day beyond doubt that DNA is a large-molecule chain type matter that (except for some vira) transmits the hereditary informations from cell to cell and, in the course of the increase of the organisms, from parent to progeny. Some sections of the DNA chain can be already considered as essentially identical with the units of hereditary transmission, the genes. Thus the two spiral and scalar constructions of DNA (Fig. 1.) to all probability already represent the two opposite sexes, as evidenced at least by experiments with bacteria.

Such conditions might have prevailed in the history of the Earth about two to three thousand million years ago in the so-called azoic age.

Stage III. Anucleophyta

a) Bacteria

Evolution of the terrestrial life and the conquest of the continents essentially begins when the inorganic matter that became living assumes a cellular structure but no definite *nucleus* or chromosomes are developed in the cell as yet. The most characteristic representatives of this stage are *Bacteria* and blue algae *(Cyanophyta).*

The vegetative propagation of *Bacteria* occurs in the simplest way by simple division. When the individual divides in two parts, two individuals of the same kind develop from each half as that from which they themselves derive. This process then reiterates in an infinite number of cases, while the progeny remain both morphologically and physiologically equivalent to each other. The *Bacteria* do not possess a definite *nucleus* as yet, only a diffuse, protein type substance in which thymonucleic acid, DNS, is the most important compound and which to all probability has already a certain role in transmission by heredity. According to most recent investigations, in *Bacteria* already pairing occurs to a certain extent (Fig. 5.) which may be considered as a primitive manifestation of sexual propagation. But if there is sexual propagation, it can be traced back to the contrasting F+ and F— nature of the protoplasms or protein type compounds of the two merging cells and to the receding in distance of the two lines of the DNA spiral or their completion respectively (Fig. 4.). Thus among the *bacterium* individuals besides the chemical dimorphism some kind of sexual dimorphism, a physiological dimorphism takes shape, which appears more distinctly in the plants of cellular and nuclear structure.

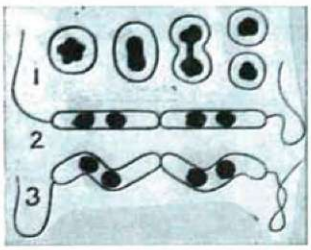
b) Cyanophyta

Essentially the same phenomenon is observed in Cyanophytes where in cell division central protein type particles and others suggestive of *nuclei* are forming. No perceptible sexual reproduction is known though in Cyanophytes; the separation of the *nucleus* type substance comes to pass in a very simple way, by

Stage III. ANUCLEOPHYTA

Fig. 5

Fig. 4



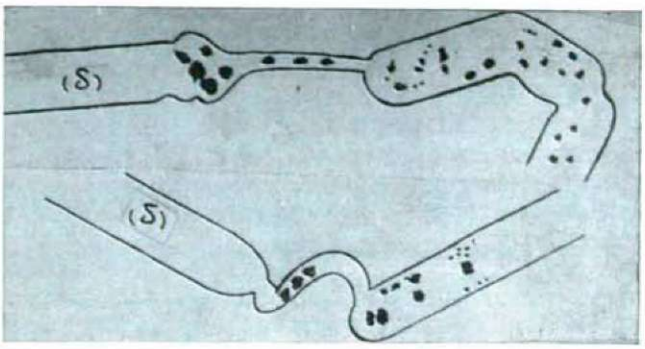


Fig. 6

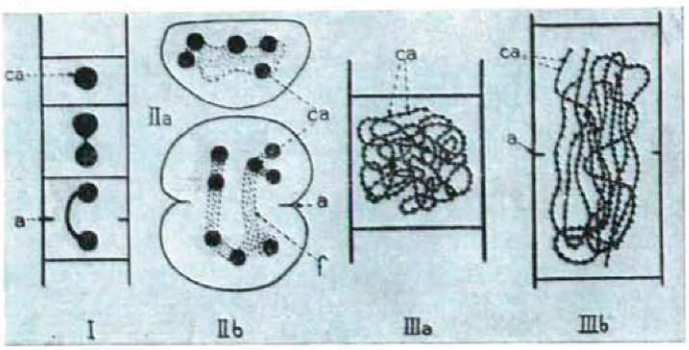


Fig. 4. The 3 types of *Bacteria*. In the cells black details mark the chromatinomous substance and its differentiation (According to CHADEFAUD).

Fig. 5. *Bacillus megatherium*. Between the two cells a conjugational canal forms. (According to CHADEFAUD, drawing after the photograph of LAMATER).

Fig. 6. *Cyanophyceae*. In the cells the chromatinomous substance (ca) is indicated by the details in black. I. *Oscillatoria terebriformis* (AG.) GOMONT. II. *Choococcus helveticus* NAEG. III. *Phormidium Retzii* (AG.) GOMONT; *ca* chromatinosomes; the place of cell division is *a* (According to CHADEFAUD).

division (Fig. 6). The so called sexual chromosomes representing the sexual character did not develop either, so that sexuality can be traced back at best, similarly to the phenomena observed in *Bacteria*, to the effect of the two lines of the DNA spiral. All parts of the cells developed in division are completely equivalent both from the morphological and physiological points of view. It is incompletely understood whether a sexual dimorphism exists or not among Cyanophyte individuals; but a chemical sexual dimorphism may be surmised on the analogy of *Bacteria* to all probability.

Such conditions might have prevailed in the azoic age of the Earth in the so-called Praecambrium, about 1000 million years ago.

Stage IV. Monadophyta

In the unicellulars with cell nucleus, the Monadophytes, a more developed state of sexuality appears more markedly and a further step can be noted as against the previous condition. All unicellular organisms may be generally designated as *Monadophyta,* irrespective of whether they belong to the various systematic groups such as *Flagellatae* or *Chlorophyceae.* Among the unicellular organisms besides the asexual, simple division, various degrees of the manifestation of sexuality can be observed which could have been developed only from the previous forms. These developmental stages are *isogamy, homogamy* and *anisogamy.* When Unicellulars are merging with each other, they can be already considered virtually as sexual cells, which are either *isogametes,* or *homogametes* or *anisogametes* (heterogametes). Those unicellular individuals which separate into both physiologically and morphologically equivalent gametes may be called *isogametangia,* as well, whereas those in which morphologically identical but physiologically different pairing cells arise, *homogametangia* and finally those in which morphologically different minor or major gametes develop, *anisogametangia.*

Isogametes

The isogametes are morphologically entirely, but physiologically only nearly identical. In these organisms the two kinds of sexual character is present to an equal extent; the chromosomes representing sexuality, to all probability did not develop yet; it seems that DNA, the compound determining the sexual character, did not separate yet in distinct chromosomes, but it is already present in the same *nucleus.* Whenever vegetative division of the individuals takes place in the two individuals that originated not only the particles of the protoplasm but also the compounds carrying sexuality, so the isomeric DNA too are equally localized. When, on the other hand, fusion takes place, amphoteric individuals both morphologically and physiologically, i. e. also as to compounds entirely equivalent arise at division. This is the same phenomenon as observed when from the interaction of acids and bases a neutral salt develops. Among the Flagellates this is a rather common phenomenon. E. g. the zygote of *Stephanosphaera pluviatilis* in condition of rest at the reduction — division within the hermaphrodite cell separates into gametes which are morphologically similar, but physiologically likely to be dissimilar and which unite still within the mother cell. Thus the individuals can be considered essentially as monoecious.

Homogametes

It marks a higher degree of evolution, when the individuals or gametes though externally equal and similar to each other, are physiologically already definitely different. In these organisms the DNA determining the sexual character in reduction division segregates in two contrasting isomers, as was seen in *Bacteria,* so that half of the gametes developed received DNA representing + character, while the other half got DNA of — character. Simultaneously also the so-called sexual chromosomes which are carrying them, have separated

(*haploid* section). These *haploid* individuals after vegetative division never unite with individuals carrying the same sexual character but only with the opposite ones. This is evidenced by the fact that if these individuals repeatedly form *gametangia,* the individuals (gametes) developing from these always become united with gametes arising from the different individuals, never with their „twins". The originating diploid *zygote* either continues to float (planozygote) or losing its cilia immediately retires to rest and transformed at the reduction division into *gametangium* separates in two male and two female individuals with physiologically different (positive and negative) chromosome sets *(Chlorogonium euchlorum, Ch. elongatum, Ch. neglectum, Gonium pectorale.* — Fig. 7). These two kinds of individuals (gametes) are morphologically entirely identical and differ only physiologically, so they are dioecious. The physiological difference to all probability must be traced back again to the influence of DNA, possibly upon the effect of the more intensive light. Thus these gametes substantially differ from the *isogametes* and therefore may be regarded as *homogametes,* whereas the individuals engendering them, as *homogametangia* at the time when they do engender them. The homogametes or *homogametangia* respectively represent the second developmental degree as against the isogametes or *isogametangia,* i. e. the dioecious form against the monoecious. Several examples of this are known also from the Flagellates.

Anisogamy

Evolution made a further step by the realization of *anisogamy.* In this developmental stago the gametes not only physiologically but also morphologically differ from each other, i. e. sexual dimorphism subsequently to the dimorphism of chromosomes has spread to the morphology of individuals, essentially also to the form of the gametes, so that *gamete dimorphism* ensued (Fig. 7). A number of classic examples are known for this particularly in *Chlamydomonas* and *Chlorogonium (Chlamydomonas fonticola, Eudorina elegans)* and in some cases evolution goes so far that the cell content of the one individual actually develops into a true immobile ovule *(oogonium)* in *Chlorogonium oogamum* while the other cell disintegrates into an infinite number of biciliate, so-called microgametes (Fig. 7). Consequently, already here the stage of historical evolution occurred in which the female gamete has finally lost its mobility, became immobile and maintained this condition of immobility during the history of evolution even in the most developed terrestrial phanerogams. The male gametes, however, retained mobility with the aid of their cilia as long as fresh water has been the medium between the two kinds of sex and had lost this capicity only when in the gymnospermous and angiospermous condition wind and insects took over the mediatory role.

The essential in the Unicellulars is, consequently, that the individuals are either monoecious and, when pairing *isogametes,* or dioectious and when they unite either *homogametes* or *anisogametes.* The establishment of these three developmental stages as soon as in the unicellular condition is the more important because it repeatedly occurs according to the same pattern in the history of evolution of the vegetable kingdom. It had to repeat itself by necessity, because it is the fundamental law in the history of evolution of sexuality.

Evolution makes a further step e. g. in the case of *Eudorina,* when separate male colonies develop, breeding spermatozoids, while in another colony only

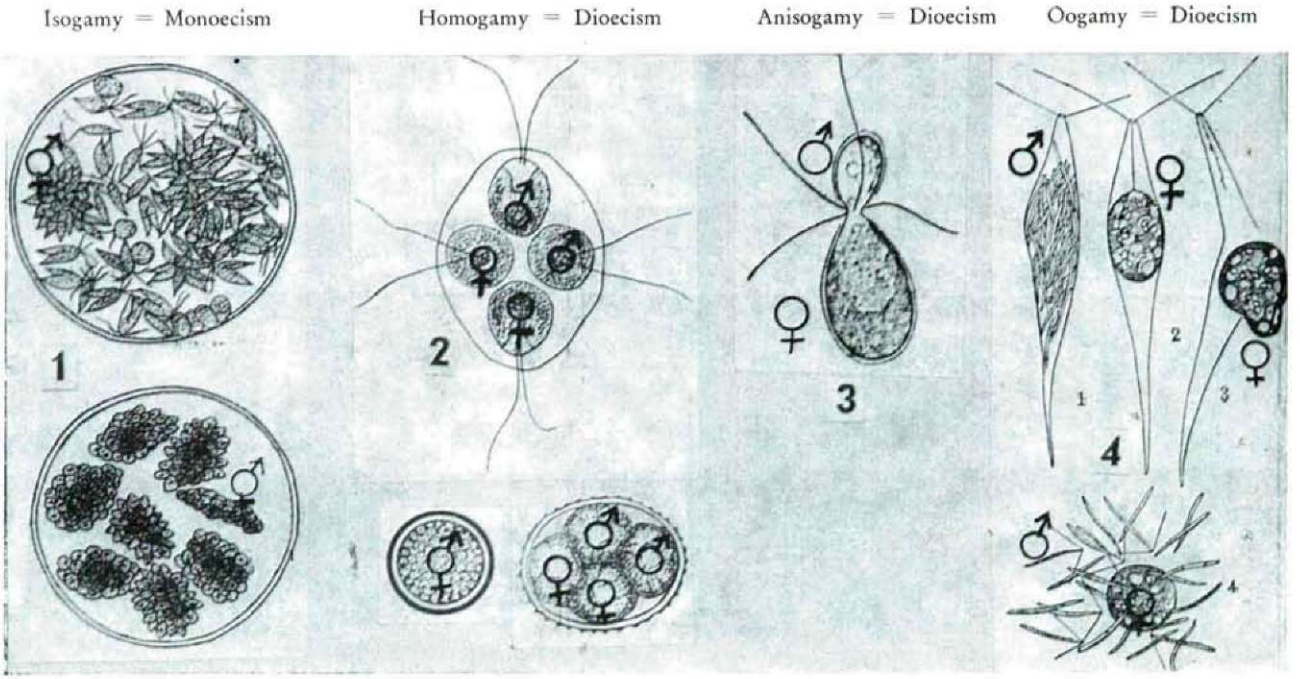


Fig. 7. *Isogamy* of *Stephanosphaera pluviatilis* within the cell wall. II. *Homogamy*. 2 male and 2 female type homogametes of *Gonium pectorale* within the cell. From the zygospore by reduction-division 4 gametes arise from which 2 are of male, 2 of female type; they are morphologically equal and differ only physiologically, so they are homogametes. III. *Anisogamy*. *Chlamydomonas fonticola*. The smaller is the microgamete, the larger the femaletype macrogamete. IV. *Oogamy*. *Chlorogonium oogamum*. 1. In the male-type individuum a great amount of spermatozoids, 2. in the female-type individuum a single immobile egg, 3. egg emerging from the cell, 4. the egg is surrounded by many spermatozoids.

individuals, gametes of female character develop. The spermatozoids released from the male *gametangia* surround the female colonies, uniting with and fertilizing them (primitive allogamy). The result of the fertilization consists in several unicellular zygotes which secrete a thick wall around themselves to start, after a certain period of rest, reduction-devision. From the 2 male and 2 female individuals (tetrades) originating thus only one develops further while the three other brothers degenerate. Accordingly, the remaining fourth individual can be either of male or of female character. In the final result half of the zygotes developed from the female colonies, assumes a male the other half female character. Hereby the sexual dimorphism advanced again by a step because physiological dimorphism appears now not only among the colonies, i. e. cell groups but also between zygotes.

Essentially the same process occurs in the dioecious *Volvox dioicus*. Also in the *Volvox* monoecious and dioecious colonies occur *(Volvox globator)* among whose vegetative cells *antheridia* of male character and *oogonia* of female character appear. The spermatozoids ripen earlier than the eggs and only exceptionally fertilize their own egg, when autogamy ensues (though allogamy is more general). In the dioecious forms reduction-division of the zygote occurs whereas the zygote of the monoecious forms after the first heterotypical cell division immediately develops into monoecious colony.

In Flagellates — as shown above — the condition of *Volvox* and *Eudorina* is most developed where sexual differentiation is realized not only between the individual gametes but also between colonies. Spherical cell association trend seems to have reached herewith its highest degree; it actually did not develop further, the developmental trend simply came to an impasse.

Besides the spherical cell association form nature tried out also another potentiality, when the cells after their divisions rallied not in spherical colonies but in cell-filaments and lamellae. Evidently this direction was more suited for evolution because starting from the unicellular organisms a further evolution ensued, and first the cell filament than the cell lamellar and cell corpuscular *Algae* developed (Fig. 8).

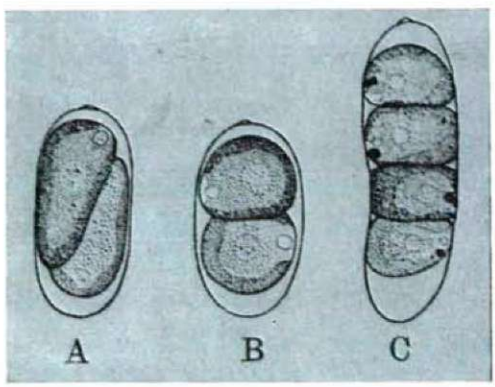


Fig. 8. *Chlamydomonas seriata*. The zygote first divides with an oblique wal in two parts. *A)* the oblique wall subsequently assumes a horizontal position *B)* then it repeatedly divides with a horizontal wall and hereby a short cell-row originates. *C)* The simplest pattern of cell filament formation. According to. PASCHER.

The problem of sexuality

In connection with the phenomena observed so far the question arises, why do gametes of different sex, organs of reproduction or individuals of different sex develop in nature, one of which exhibits male (+) the other female (—) character and generally what is the reason why invariably gametes and reproductive organs of two opposite sexes arise which phenomenon is manifest not only in the simplest living beings in the *Bacteria* and in the most developed plants but in all living organisms. This question, the problem of the transmission of sexuality by heredity materializes in the strict regularity of the sexual propagation of living beings. Why is it that in nature once male, then again female individuals or two kinds of mating cells originate and that only these unite with each other?

Already MENDEL observed that sexuality is an inherent property of living beeings, exactly as e. g. size, colour or shape of peas. Recent research work revealed that besides the determining role of DNA, properties connected with sexuality are always linked in the *nuclei* with one or two chromosomes of definite size — the shape and size of which, however, is different from the others — the so-called *sexual chromosomes* or *heterochromosomes*, and that the sexual properties of the individuals are always transmitted to the progeny through the instrument of these, as if all properties related to the sexual character were localized in these special chromosomes. In all plants and animals which are heterogamous and even in man, when the sexual cells develop, in the *nuclei* besides the other vegetative chromosomes (autosomes) one or two so-called sexual chromosomes (x or y) are formed (Fig. 9). These sexual chromosomes are responsible for it, among others, that now male now female individuals develop and that certain properties are linked to one sex or the other. Why is it important to

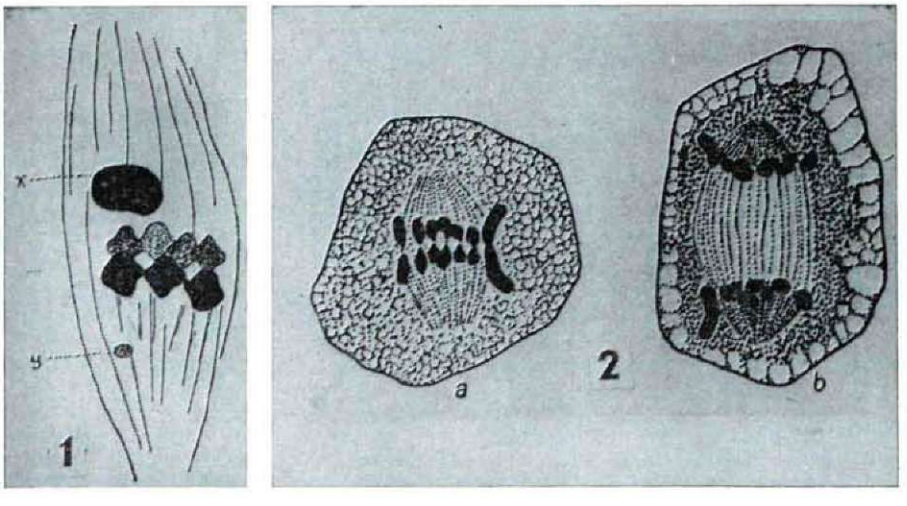


Fig. 9. *Spherocarpus terrestris (Musci).* In the metaphase of reduction-division X and Y chromosomes. First division of the pollen mother cell of *Melandrium album* (reduction-division) *a)* early, *b)* late anaphase, with separation of the X and Y chromosomes (according to HARTMANN).

stress this regularity in the evolution of the vegetable kingdom from the very beginning, in the discussion of the simplest plants? Because in most of the living beings invariably such individuals or organs of propagation develop in which the sexual character always manifests itself in the appearance of the reproductive organs and in the finer structure of the gametes developing in them.

The simple explanation of this phenomenon materializes in the fact that in the *nuclei* of the sexual cells of all heterogamous individuals at the origin of the sexual cells always a certain number of *n* chromosomes appear from which one is invariably the socalled *sexual chromosome* (x), while in the vegetative cells, the so called autosomes, the double number originates (nn + xx). This sexual chromosome has a different shape and size both in the male and female gametes. For instance in the vegetative cells of the female individuals (FF) there are a certain amount (2n) of chromosomes and two identical,' so called homologous sexual cromosomes (xx) (Figs. 10., 11). As a contrast, the male individual also

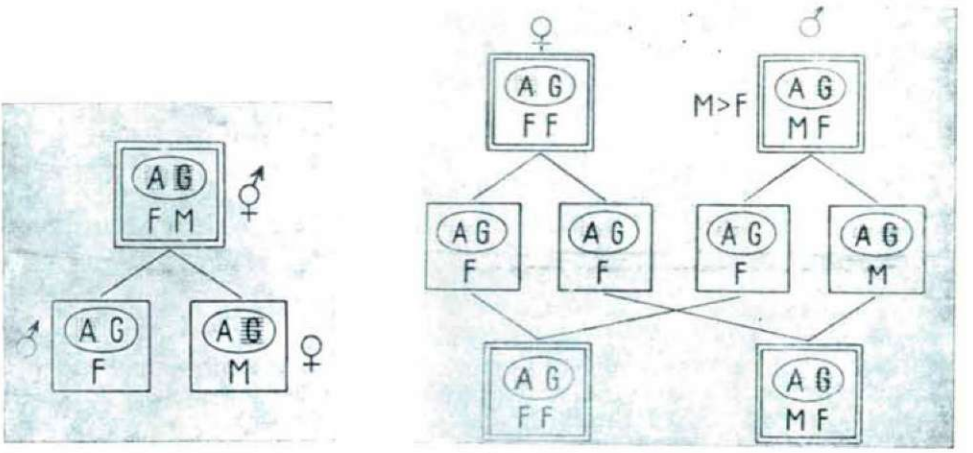


Fig. 10. The scheme of the haplogenetic sexual determination e. g. in a dioecious moss. A and G mark the male and female potentials. F is the realizator directing the female trend and thus limiting the development of the male trend. M is the realizator of the male trend. In diplophase (in the sporophyte above) F and M are also present. M is the male realizator which prevents the female G potential from developing; therefore G is cancelled (similarly the female realizator F inhibits the male potential, therefore A is cancelled with dotted lines). In reduction-division one gone contains only F the other only M, whereas both contain A and G. Consequently in the one case (left) F inhibits only A and as a result the gones or spores and the gametophyte derived from them will be female. In the gone which contains M, only G will be inhibited, consequently the result will be male. (According to GUTENBERG).

Fig. 11. Diplogenetical sex determination in Phanerogams, according to the *Bryonia* experiments of CORRENS. In all individuals male and female potentials (A and G) are localized. All female individuals contain in a homologous pair of chromosomes a female realizator F so they are homogametes of female trend. As a contrast the males contain two different realizators, namely a female determinator F, and a male determinator M, so the males are heterogametic (first row of the sketches). Consequently in reduction-division in all pollen mother cells two of the four pollens are of the F and two of the M type (2. row). At the fusion of the sperms with the egg when those containing F realizators are fertilized, from the fusion of F with + F a female plant arises. If on the other hand M merges with F, a male individual originates, since the trend inherent in F is stronger than in M. Lower row of the sketch (According to HARTMANN).

contains 2n autosomes and besides x or x and y sexual chromosomes (MF). Accordingly in reduction-division most female individuals produce only one kind of sexual cells, i. e. gametes of female character (n+x) (F); this is why the female individuals are generally *homozygous* (FF). Most male individuals on the other hand are heterogametic (F and M) because they produce two kinds of sexual cells namely n+x and n+y or only n gametes. If e. g. the homozygous egg (F) (n+x) is fertilized by a male sexual cell of a similar chromosome set (F) (n+x) female individuals (FF) (nn+xx) would originate whereas if the homozygous egg (F) (n+x) is fertilized by a different heterogametic sexual cell (M) (n+y), male individuals (MF) (nn+xy) would originate. Thus sexuality is determined in the first place by the sexual chromosomes and by DNA activity localized in them. And since in reduction-division gametes determining the two kinds of sexes originate to an equal ratio (50 : 50 per cent), this is the explanation of the fact that in the vegetable but also in the animal kingdom the two sexes are represented more or less at an equal rate. This regularity which is based on strict cytological foundations had an important part in the course of the evolution of plants; it is a phenomenon accompanying evolution from the unicellular organisms to the most developed forms of the vegetable kingdom, the *Angiospermae* of the Phanerogams. Such aspects should determine our view of the phenomena related to sexuality among the unicellular organisms. Although nature had accomplished a wide range of variability among the unicellular organisms as to the aspects and transmission by heredity of sexuality, still in the final result all this must be traced back to the three ancestral types i. e. isogamy (monoecism), homogamy (dioecism) and anisogamy, which conditions have been directed always and everywhere by the forms of opposite effect of the various compounds, and DNA in the first place. The monadophyte condition in the history of the Earth attained its highest degree in the *Praecambrium* and *Cambrium* when the four developmental stages referred to above had realized in incredibly manifold forms which is verified also by the infinitely varied forms of the recent freshwater and sea Unicellulars.

Stage V. Algophyta

Multicellular state.

After this short digression let us revert to the unicellular organisms. The plant kingdom did not remain in this simplest unicellular state. The next step in evolution during a „try-out" of many million years was the *association of cells,* when the dividing cells after having originated did not completely separate from each other but remained in further contact and connection in colonies, cell-families, beside oneanother. This juxtaposition has been realized in the form of *cell filaments, cell-lamellae* (cell bodies) or *spheres.* In all three directions the division of sexuality again continued in the ancient three types of *isogamy* (monoecism), *homogamy* (dioecism) and *anisogamy* (oogamy). *Volvocales* exhibit the spherical degress of evolution *(Pandorina, Eudorina, Volvox)* while the possible evolutionary degrees of the cell filament and lamella state materialized within the *Chlorophyceae* (in the *Ulotrichales, Siphonales* types) with a great variety. It seems, however, that the sphorical trend was not a form suited for further evolution and reached its peak in *Volvocales;* instead or

besides the filamentons, laminar and cell body trends developed further because they were adapted to the conquest of fresh waters and of the continents.

Branching forms.

There is no doubt, neither can be, that the unicellular plants derived from the multicellular and, as referred to above, initially from the spherical or filiform types respectively. The filiform type might have originated from the exceedingly varied unicellular organisms by repeated branching (*Vaucheria*, Fig. 12); or else the cells originating as a consequence of the one-way division

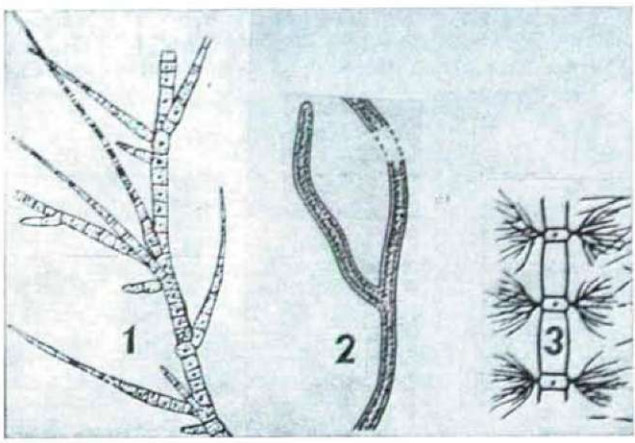


Fig. 12. Three types of branching in *Chlorophyceae*. 1. *Stigeoclonium subuligerum:* monopodial. 2. *Vaucheria sessilis:* dichotomous. 3. The whorled branching in *Drapalnaldiopsis indica*. The stages of development are identical, still there are three types of branching. (According to PASCHER and CHADEFAUD).

formed cell filaments *(Cladophora, Ulotrix Drapalnaldiopsis)* thus giving rise to organisms of primitive structure branching in different ways. Any kind of branching consists in an increase of surface which is favourable for the vegetative life of the plant; at the same time a possibility arises for cells and organs to come into being which would assure the production of progeny.

It should be noted here that the various forms of branching started right from the unicellular plants and this trend as a basic principle remained up to the most developed plants. Since in our view, branching has a decisive role in the history of evolution of the vegetable kingdom, this problem must be briefly dealt with in order to facilitate understanding of what follows.

When the cells divide in one direction of space with transversal walls or possibly with apical cells, actually non branching cell filaments originate. Several such forms are known among green algae (*Spirogyra, Zygnema, Ulotrix* etc.). Branching occurs when the cells or cell-groups formed increase in two or three directions of the space and in the meantime assume various forms.

Some unicellular *Vaucheria* e. g. are branching repeatedly and dichotomically. This is the *dichotomical* branching. In the filamentous algae *Cladophora, Bulbochaete* at the meeting of the terminal cell-walls lateral filaments originate which, however, are always younger and less developed than the main branch

from the side of which they came into being. Thus here a central *axis (monopodium)* exists from the side of which the lateral branches originate. This is the *monopodial* branching (Fig. 12).

The filamentous *Drapalnaldia* or the recently discovered *Drapalnaldiopsis indica* also have a central filament axis which, however, consists of regularly short so-called nodial and much longer internodial cells. From the short nodial cells, i. e., from the same height, several secondary but equivalent lateral filaments originate. Consequently this branching essentially differs from the first two, from the monopodial and dichotomous. This ancient primitive form of branching is termed as *whorled* or *verticillate*. Comparison of the three forms of branching reveals that all three are characteristic to such a high degree according to the author on this degree, that none can be derived from the other. The attempt to derive monopodial branching directly from dichotomical branching by an overgrowth of branch is not valid and lacks all positive evidence. Similarly the verticillate branching can not be derived either from the monopodial or from the dichotomical. All three kinds of branching are ancestral types the simplest form of which can be found even in our days among the fresh water algae of filamentous structure. This phenomenon also proves that the evolution could have started from the unicellular condition towards the filamentous stage in the fresh water at the very beginning in several directions, i. e. the trend of evolution within the green algae could have been polyphyletic right from the beginning.

To this finding it should be immediately added that the same types of branching are realized in sea weeds which supports the assumption that the further development of the branches of fresh water algae could have occurred independently of the development of sea weeds. Among sea weeds too these three types of branching have materialized because only these three main types are possible. But to whatever branching type the fresh water Algae may belong, they agree in that the gametes assuring sexual reproduction form on the same individual, when they are monoecious, or on two similar individuals, when they are dioecious, or on two individuals of different form (anisogamy). All three developmental stages within the Algae are actually replicates of those fundamental states which were observed in unicellular organisms except for the sexual acts having been already transferred from the single cells — as a consequence of division of functions among the cells — to more developed states assuring better possibilities for further evolution, namely to the cell filaments or lamellae, cell bodies respectively.

In the monoecious, multicellular, filmentous individuals the haploid gametes of the same size and of opposite chemical character merge in the water into an unicellular diploid zygote which unicellular zygote after a shorter or longer state of rest undergoes a single reduction division and the haploid cells formed grow into haploid cell filaments. The sporophyte — i. e. the diploid generation — is in this case only unicellular (1) as against the gametophyte that possibly consists of an infinite number of cells (∞). Thus from the zygote only one kind of filoments develop which are of hermaphrodite character. This is observed e. g. in the monoecious green alga *Acrohaete repens* or in the monoecious *Oedogonia* or in the monoecious *Bulbochaete* (Fig. 13).

In the dioecious filamentous algae the position is essentially the same, with the difference that here male and female gametes are produced by different

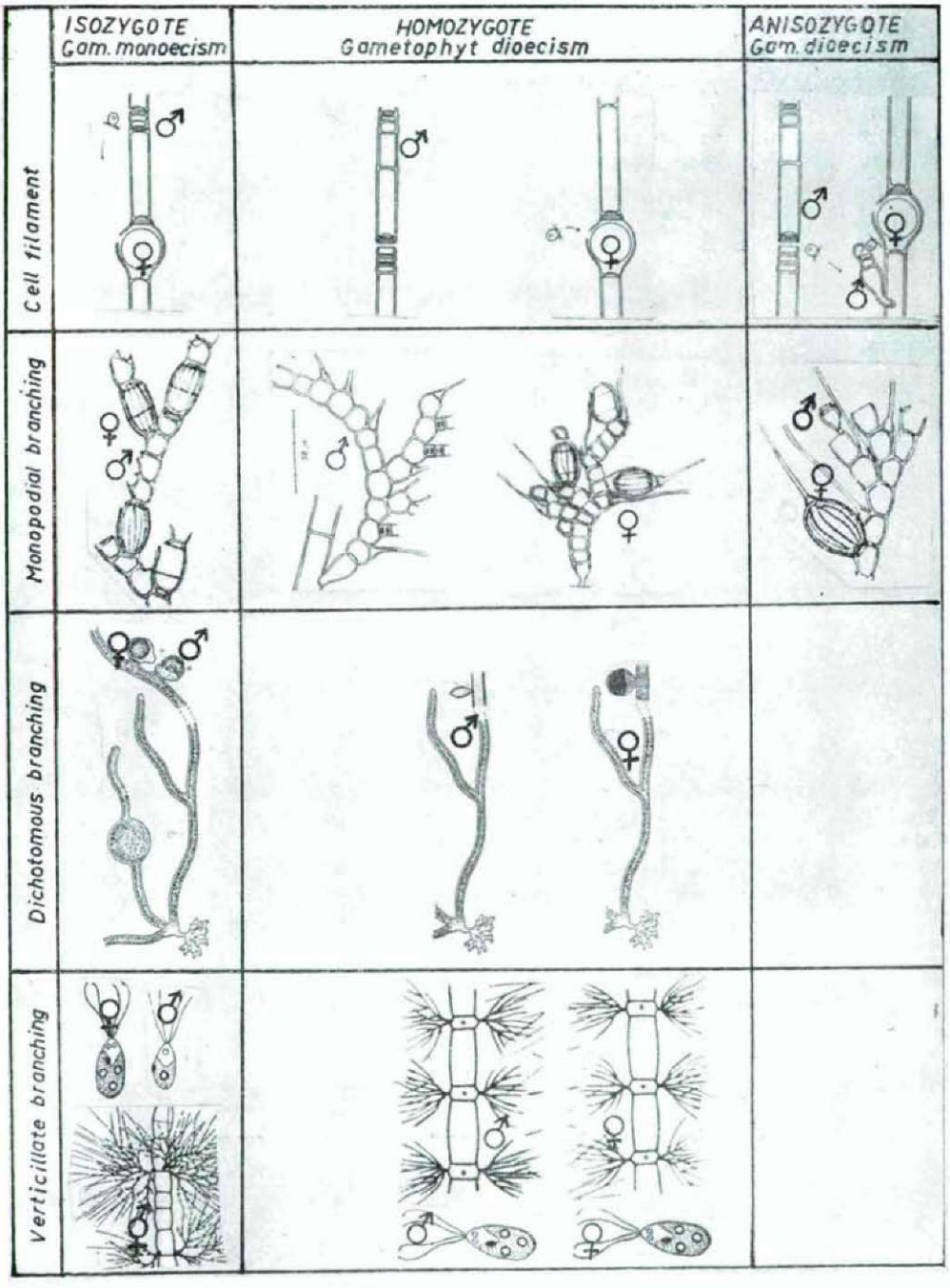
filaments. Both filaments and gametes are morphologically similar to each other and exhibit only physiological differences. From the fusion of morphologically similar but physiologically different haploid gametes in this case too only a unicellular diploid zygote arises which for a shorter or longer period goes to rest to give rise subsequently after reduction division to half male half female type but morphologically similar filamentous individuals from the haploid cells. These zygotes are morphologically completely identical (isozygotic) and differ only cytologically, namely in the different chromosome structure from the isozygotes. Therefore they are called, to distinghish them, on the analogy of the term homogamete: homozygotes.

This stage of development is realized particularly in the dioecious *Bulbochaete, Oedogonium, Vaucheria,* in the dioecious, *Drapalnaldia.* The + and — character is induced also in these cases, to all probability, by the compounds determining sexuality, mainly by DNA, within the *nucleus;* these compounds are arranged and localized respectively in the so called sexual chromosomes that determine sexuality.

Even this stage of development shows a further advance when sexual dimorphism extends to the gametophytic individuals originating the gametes and when this step is made, the multicellular filamentous gametophytic individual has not a single cell left without sexual differentiation. Thus the sexual differentiation of the gametophyton is completely realized in this state but at the same time the unicellular diploid zygote which alone represents the sporophytic phase, morphologically still completely agrees with the equally unicellular iso- and homozygote. So there is no morphological difference among

Fig. 13. *Monoecism, homomorphous dioecism* and *heteromorphous dioecism* in Chlorophyceae. *Upper row.* 1. On the same individuum of the monoecious *Oedogonium nobile* WITTR. the polyciliate male spermatozoids and the egg (monoecism) develop. 2. Homomorphous dioecism in *Oedogonium capillare* (L.) KÜTZ. In the one male individual the polyciliate spermatozoids while on the others which are similar to the male individual, only the eggs (oogonia) develop. 3. Heteromorphous dioecism in *Oedogonium diplandrum* JUR. In the one male individual androspores arise from which a few cells high dwarf males originate; these settle in the vicinity of the female *oogonium* and their gametes fertilize the egg (oogonium).
2. row. Monopodially branching cell filaments. 1. Monoecious *Bulbochaete.* Some cells of the cell filament develop into *oogonia* while others to *antheridia.* Thus the individual is monoecious. 2. A male plant of *Bulbochaete annularis* and a fernale plant. Dioecious macrandrous species. From the two kinds of individuals of *Bulbochaete* sp. the one forms androgametes which settle on the female individuals near the *oogonia* that develop on them. Between the two sexes there is sexual dimorphism, heteromorphous dioecism. 3. Thus the individual is dioecious. The same is found in a third species where the oogonium and the antheridium of dwarf male character (♂) develop on two kinds of individuals and came subsequently into the female individual so that between them heteromorphous dioecism exists.
3. row. On the same individual of the dichotomously branching filamentous alga *(Vaucheria sessilis)* are found the *antheridia* and the *archegonia,* consequently the individual is monoecious. On one individual of *Vaucheria dichotoma* archegonia only, while on the other antheridia only develop, consequently the individuals are dioecious.
4. row. From the individual cells of the filament of verticillate branching smaller microgametes and larger macrogametes of male character develop. Thus the individual is monoecious. In the cells of some individuals of *Drapalnaldiopsis indica* swarming spores with 4 cilia of only male character and in the cells of other similar individuals 4 ciliate swarming spores of female character originate. Thus the species is dioecious. This means that also within the *Chlorophyceae* the same developmental phases occur but with essentially different branchings.

Stage V. ALGOPHYTA



the three types of zygote. Since, however, from the one (isozygote) after reduction division monoecious gametophytic filaments (first vertical row), from the other zygote gametophytic filaments of two sexes i. e. dioecious individuals (homozygote, middle longitudinal row), while from the third equally dioecious individuals of different shape arise (third vertical row), so to distinguish this third developmental stage from the homozygote we call it anisozygotic.

According to what has been said above, also in the filamentous Algae as to the distribution of sexuality three developmental stages can be distinguished, similarly to the unicellular organisms, namely the monoecious isozygote, the dioecious homozygote and the dioecious anisoxygote of different shape. All three represent the unicellular sporophytic stage as against the unicellular sporophyton.

Since we have distinguished these three developmental stages, let us now examine which way these main types materialized within the phylum Algae.

The monoecious isozygotic developmental stage occurs within the *Chlorophyceae* e. g. in the *Capitularia* with monopodial branching, e. g. in *Vaucheria dichotoma* or *Dichotomus* or *Phycopeltis* pertaining to the dichotomically branching *Siphonales* or in the *Drapalnaldia* forms of verticillate branching. In all three the developmental stage is the same, monoecism, still the branching is strictly of three or four different types. The assumption seems justified that these types have reached the same developmental stage, monoecism, independently from each other, thus to get so far they had set off, starting from the Unicellulars, probably from three directions (monopodial, dichotomous and verticillate).

Exactly the same applies to the homozygote. Most of the *Vaucheria* are dioecious. Similarly, from the *Drapalnaldiopsis* with verticillate branching rather many are dioecious, but also in *Ulotrices*, *Oedogonia* and *Bulbochaete* dioecious forms are known. Consequently the filamentous algae have reached also the dioecious stage from three or four directions.

A still more developed state materialized in the dioecious *Oedogonium* and *Bulbochaele* by the development of dwarf males where two gametophytes of different shape and size come into being. The zygote, however, is again unicellular, giving rise by reduction division to gametophytes of two different sizes and forms, thus it is *anisozygotic*. According to these facts, sexual dimorphism materialized in a striking manner among the gametophyton individuals, while the zygote remained unicellular.

Homomorphous alternation of the two generations.

Within the Algae development made a further advance, since in some cases so called homomorphous individuals arise, i. e. both gametophytes and sporophytes are quite similar to each other. The sporophytic individuals of the morphologically entirely similar *Cladophora* are completely analogous as to their morphological aspect, but physiologically they give rise to two types, + and — of four ciliate so called zoospores from which again morphologically identical dioecious, i. e. + and — gametophytes originate. One of these forms positive (male)-type while the other negative (female)-type two-ciliate gametes. The haploid gametes at first unite to form diploid zygotes; these, however, do not remain in a state of rest, but develop into diploid individuals quite similar

to the haploids and as such give rise in some of their cells by reduction division to two types of (+ and —) four-ciliate zoospores. Exactly the same homomorphous developmental stages materialized in the recently discovered *Drapalnaldiopsis indica,* with the essential difference, however, that *Cladophora* is a filamentous green alga with monopodial, while *Drapalnaldiopsis* with strictly verticillate branching. Thus again the same developmental stage and identical alternation of generations are found, but in the one case it is a filamentous green alga with monopodial, while in the other with verticillate branching. The two algae arrived from different directions at the same developmental stage. Probably also in *Hepaticae* such phenomenon occurs, although it had not been observed yet so far. In the above developental courses most probably already such a phase can be seen. (Fig. 14). Thus here already a phase appears that will repeat itself essentially in the evolutionary history of the terrestrial plants, marking somehow the further path of evolution. These are the so-called homomorphous individuals. Most probably this phenomenon materialized also in the *Psilophyta* of the Devonian (see later).

The further march of evolution is indicated within the *Chlorophyceae* by the *Coleochaete* species which are monoecious, thus developing one type of individuals which give rise to *antheridia* from which male gametes arise and to *oogonia.* The zygote formed from the fusion of haploid gametes secretes a thick wall, subsequently remains for a certain time period in state of rest and then first produces a reduction division within the thick wall, to divide later into 8 to 16 cells *(C. scutata).* In the dioecious individuals of other species, however one of the gametophytes is a male one and develops *antheridia* the other is a female one; thus the individuals, the gametophytes are sexually entirely differentiated, but the zygote is hermaphrodite. It is an important development here, that the wall of the zygote is thickening, becomes surrounded by cortical cells; we might even state that it transforms into a *sporangium,* because in its interior by reduction division haploid cells arise, which are entirely homologous with the spores of vascular plants. This phenomenon starts a new developmental trend in the vegetable kingdom, which began to materialize progressively at the beginning of terrestrial life in the developmental stage of the Mosses, probably already in the Cambrian.

Thus for the fresh-water filamentous algae it can be established that the three developmental stages appear according to the same pattern as has been observed in the unicellular organisms, since in the distribution of the reproductive organs again monoecious, dioecious and dioecious heteromorphous individuals originate. The zygote is still unicellular, but already exhibits physiological differences (isozygotes, homozygotes and anisozygotes respectively). It is a further important circumstance that these three developmental stages equally occur in the monopodial *Siphonocladales,* in the dichotomous Siphonales *(Vaucheria)* and in the *Drapalnaldia* and *Drapalnaldiopsis* of verticillate branching from which again the probable inference may be drawn that the origin of the fresh water Algae might have been polyphyletic right from the start as unicellular organisms. This cell-filament stage must have been realized in the Praecambrium and Cambrium age of the Earth. From that age a great number of filamentous Algae remains came to light and which developmental grade was preserved by many fresh-water filamentous algae until our days.

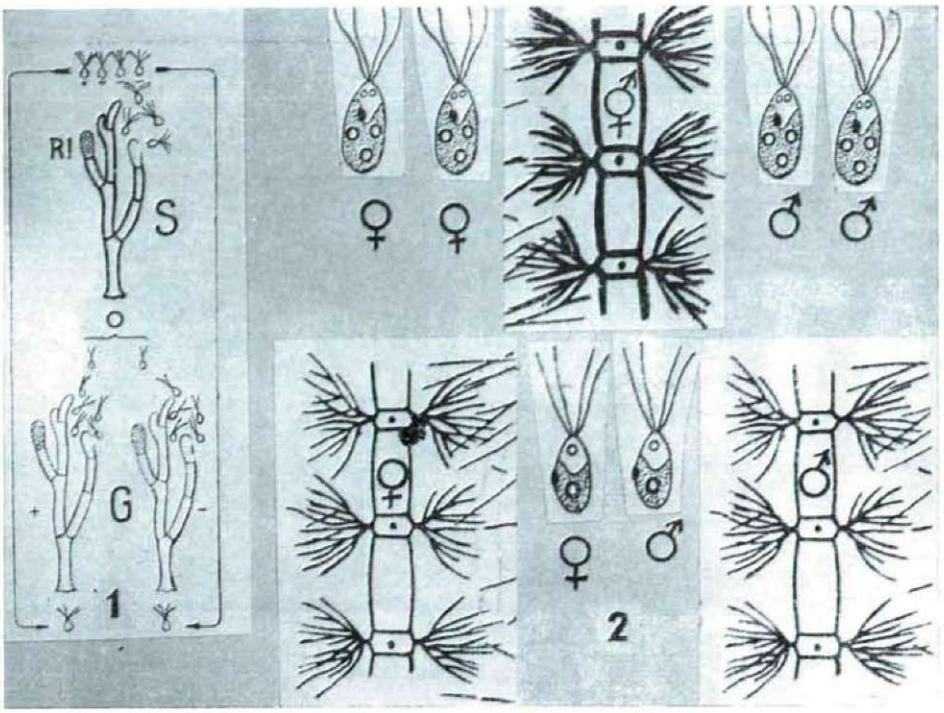


Fig. 14. Homomorphous alternation of generations in *Cladophora glomerata (Siphonocladales).* The gametophyte (G) is dioecious, morphologicaly entirely identical with the diploid sporophytic phase. This is one of the initial phases of the transformation into multicellular of the diploid phase.

An entirely similar change of generations is found in the development of *Drapalnaldiopsis indica.* The gametophyton filaments of male and female character develop gametes of male and female character from the fusion of which a hermaphrodite sporophyton entirely similar to the gametophyton arises. In the individual cells of these by reduction division 4 ciliate male or female swarming spores develop.

Stage VI. Bryophyta and Charophyta

After having examined the patterns of reproduction and the phylogeny of the *Thallophyta* s. l. we propose to review the position in the terrestrial and aquatic cormophyt plants. In these the manifestation of sexuality and the so-called alternation of generations which was rather concealed in the organisms dealt with so far-, becomes more explicit and conspicuous. Essentially, however, the picture is the same, since both among the liverworts and the *Musci* there are also individuals whose reproductive organs — here already well developed *antheridia* and *archegonia* — either develop on the same individual, so that the individuals are again *monoecious,* and accordingly the spores are both from the morphological and the physiological point of view completely equivalent i. e. isospores, or the individuals are *dioecious* and accordingly the spores are,

though morphologically identical, physiologically different, i. e. *homospores*, or there are morphological differences, consequently sexual dimorphisms even among the spores and individuals of the dioecious individuals and accordingly the spores are anisospores.

Isospore and isosporangium.

The spore from which only one kind of moss-individuals arise is called *isospore*, while the sporophore in which the isospores originate: *isosporangium (isosporogonium)*. Generally in the following all reproductive cells which develop by reduction division i. e. asexually and always at the end of the asexual process or before the beginning of the sexual process, will be termed as spores. In the Mosses the sporophytic phase originating the spores and the *sporangia* that develop on them are both morphologically and physiologically completely similar to each other and thus *isosporangia*. In the most primitive form in these *isosporangia* only such spores develop as carry in themselves both the male and the female character, so they are actually hermaphrodite spores. In these hermaphrodite spores the sexual chromosomes determining the sexual character are present though but not separated yet from each other, since in all spores originated both sexes or the DNA determining the sexual character are present at an equal rate and separation only begins when on the monoecious in this case the *sporangia* are *isosporangia* and the spores developing in them gametophytic generation the reproductive organs — *antheridia* and *archegonia* — develop on the same structure or on little separate branches. Consequently *isospores* (Fig. 15. 1).

This phenomenon also essentially coincides with the condition in which in the unicellular organisms within the single zygote cell two types of individuals, gametes arise, or when on the same individual of the filamentous Algae equally male and female types of gametes develop; the cell filament is thus monoecious. In all three periods of evolutional history the essence of monoecism is the same, although in the multicellular filamentous Algae and *Charophyta* this is somewhat more developed than in the unicellular organisms, while in Mosses the same condition appears as a consequence of the more developed alternation of generations in a still more advanced form.

Homospore, Homosporangium.

In Mosses the next developmental stage of sexual differentiation is when one spore is not sufficient to create progeny but the fusion of two sexual cells originating from a male spore and from another, female spore is necessary. Although the spores of such dioecious Mosses are morphologically quite identical, physiologically they exhibit significant differences. In the homospores the sexual character extends from the sexual chromosomes to the whole gametophytic generation, subsequently to the spores but not yet to the *sporangia*. The spores are separated from each other for the time being only cytologically (physiologically) and only in the sexual chromosomes, but not morphologically so far. The external appearance of the spores and gametophytes is entirely

similar; so is the form of the *sporangia* on the sporophyte, but in such similar *sporangia* already two kinds of spores, so called *homospores* arise, half of which (50 per cent) carries completely male character while the other half (50 per cent) is of completely female type. So in this case in the dioecious Mosses the sporophytic stage is completely similar, the *sporangia* morphologically continue to be *isosporangia* but essentially, together with the spores, they are already physiologically different, i. e. *homospores* or *homosporangia* respectively (Fig. 15, 2).

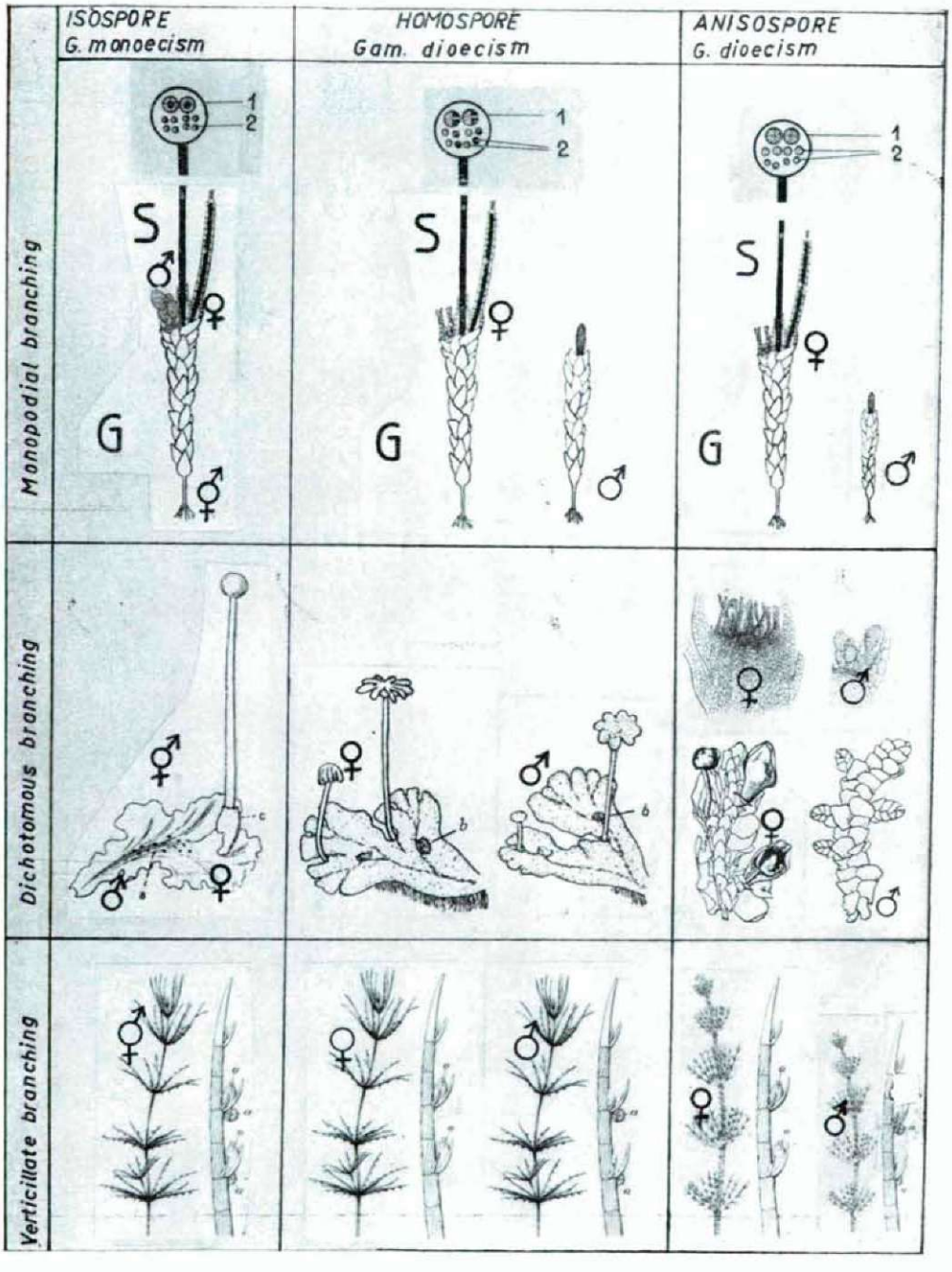
Also these conditions entirely agree with those observed in the unicellular organisms producing homogametes as well as with Green *Algae* species developing homoindividuals and homogametes. The essence is the same, the regularity in monoecism and dioecism remains unchanged.

Anisospore, Heterospore, Anisosporangium.

A still higher degree of evolution, of sexual differentiation is realized when the spores originate in the same *isosporangia* completely similar to each other but already a sexual dimorphism arises under them, since in reduction-division when the tetrades come into being always two bigger, so called *macrospores* and two smaller *microspores* take their origin, i. e. the microspores of male and the macrospores of female character develop in the same *sporogonium* (Fig. 16). Thus in the evolutionary history of Mosses the sexual, morphological differentiation made a further step, extending now to the spores representing

Fig. 15. *Isospore, homospore* and *anisospore, monoecism, homomorphous dioecism* and *heteromorphous dioecism* among *Musci, Hepaticae* and *Characeae*. 1. row. On the gametophyte of monoecious *Musci* the male-type *antheridium* and the female-type *archegonium* are on the same gametophyte. The diploid phase is monoecious, in the *sporangia* at reductiondivision hermaphrodite-type *isospores* develop, both the gametophyte and the sporophyte are monoecious. 2. Homomorphous dioecism, homospore. From the morphologically similar but physiologically different homospores gametophytes of similar form but of male and female type develop; the spores are *homospores*. On each of the monoecious sporophytes at reduction-division two homospores of different sex develop which are morphologically similar but physiologically different.
3. *Anisospore*. From the smaller male-type microspores smaller dwarf males, while from the larger spores *(anisospores, macrospores)* larger female-type gametophytes and on these *archegonia* develop. From the fertilization monoecious sporophytes arise in whose *sporangia* male type *microspores* and female type *macrospores, anisospores* develop, exhibiting different sizes and physiological differences. The *sporangia* are isomorphous, *isosporangia,* whereas the spores developing in them are of three different types viz. *isospores, homospores* and *anisospores*.
2. row. Among the dichotomously branching *Hepaticae* again monoecism e. g. *Pellia epiphylla,* homomorphous dioecism e. g. *Marchantia polymorpha* and probably also heteromorphous dioecism occur. So both in the monopodially branching *Musci* and in the dichotomously branching *Hepaticae* the same developmental stage are found. Though the developmental stages are the same, the types of branching are different. *3. row. Chara fragilis* of verticillate branching. *Antheridia* and *oogonia* are found on the same individuum, consequently the plant is monoecious. On one individual of the dioecious *Chara aspera oogonia* only, while on the other *antheridia* only develop. Homomorphous dioecism. The male individual of *Chara crinita* carrying the *antheridia* is smaller than the female individuum; heteromorphous dioecism. Among the gametophytes of the branching and non-branching green algae the same three developmental stages monoecism, homomorphous dioecism and heteromorphous dioecism occur.

Stage VI. BRYOPHYTA and CHAROPHYTA



the sexual character. This developmental stage again completely corresponds to what has been found in the unicellular organisms in the case of dioecious anisogamy and in the similarly dioecious filamentous algae in the case of dioecious anisozygoty when morphologically different individuals developed from the same zygote *(Spirogyra, Bulbochaete).*

Since the *sporangia* are morphologically still entirely equal, i. e. *isosporangia* (essentially *isogametangia*) but the spores developed in them not only physiologically but also morphologically differ from each other, so these spores, to distinguish them from the micro- and macrospores in the stirct sense of the word which should be dealt with later, are termed as *anisospores* (Fig. 15. 3).

The sexual differentiation of the spores — that has been observed hitherto in all living beings — is closely related to the biological law of the alternation of generations. The reference made to this phenomenon here is simply due to the fact that the alternation of generations appears in the Mosses in a very spectacular form.

In nature it is a general law — observed up to now in all cases — that the male sexual cells of the same individual are fertilizing the female-type cell only in the very worst case, since heterofertilization is always more successful from the viewpoint of the evolution of species. Morphological and physiological differentiation of gametes and spores is invariably the realization of this biological law.

Let us now review the pattern of realization of these four developmental stages *isospore, homospore, anisospore* and *heterospore)* within the Mosses. The phylum of the Mosses comprises the two classes *Musci* and *Hepaticae* (liverworts). The *Musci* generally present monopodial while the liverworts more dichotomous branching. Both in *Musci* and *Hepaticae* the same kinds of spores and the same developmental stages occur, i. e. *isospores, homospores* and *anisospores.* From *Musci* e. g. in *Bryales* within 466 genera about 13 334 species were found according to our investigations. From these 114 genera (24 per cent) are *strictly monoecious* (isosporous) and 242 genera (52%) strictly

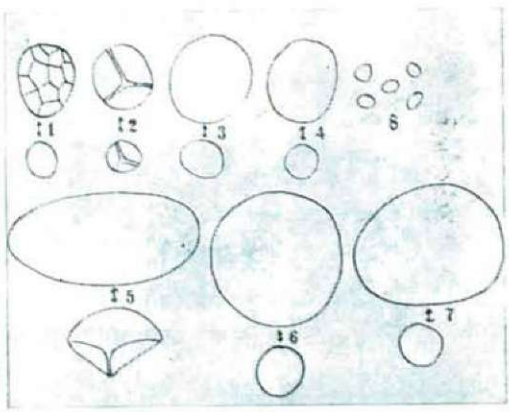


Fig. 16. The anisospores of some *Musci.* The anisospores of 1. *Sematophyllum piliferum.* 2. *Fontinalis antipyretica.* 3. *Antitrichia curtipendula.* 4. *Endotrichella elegans.* 5. *Pterobryopsis cochlearifolia.* 6. *Phyllogonium viride.* 7. *Macromitrium Blumei.* 8. *Dawsonia superba* homospores are morphologically equal, but physiologically different.

dioecious, (homosporic) and 110 genera mixed (24 per cent) i. e. occurring both in monoecious and dioecious (isosporic or homosporic) forms.

Among the *Hepaticae* dioecious species with special anisospores are rather frequent. So are e. g. the members of the genera *Fontinalis antipyretica* or *Macromitrium* where the diameter of the macrospores is at least four of rive times as large as that of the microspores (Fig. 16). As a contrast in the similarly dioecious Muscus *Dawsonia superba* all spores are exactly of the same size, so they are homospores. Another phenomenon occurring in Mosses is that in one of completely similar *sporangia (isosporogonia)* macrospores develop for the most part, while in the other microspores prevail. Moreover, in the same individual of *Brachymonium barbe montis* (Mexico) *sporangia* of two different sizes and in these spores of two different sizes are found; these are already essentially materialized *microsporangia* or *macrosporangia*. Or in the exa mined 39 *sporangia of Fontinalis antipyretica* two different sizes occur, the length raning between 4,72 and 2,65 while the wide between 1,62 and 0,92 mm. This is already a developmental stage which to a greater extent and a more explicit form is realized on a higher level than that of Mosses in the phylum of Pteridophytes *(heterosporangia)*.

Essentially similar conditions are encountered in the class of the dichotomously branching *Hepaticae*, where also both the monoecious *(Pellia)* and — mainly — the dioecious condition is found *(Marchantia)*. Although no anisosporous phenomenon was observed, still, in our opinion, it must occur, since it is a necessary stage in phylogeny.

VI. b. Charophyta

Conditions completely identical with those found in *Bryophta* occur also among the "most developed" fresh water green algae, the *Characeae*, which with their comparatively highly developed threedimensional cellular structure do not fit at all in the fresh water filamentous green algae, although the principle of the construction of their body essentially agrees with the organism of the green alga *Drapalnaldiopsis indica*. The highly developed gametophytes of the *Characeae* and their reproductive organs, *oogonia* and *antheridia*, of the same developmental stages are much nearer to the developmental stage of *Hepaticae* or *Musci* than to the simple filamentous algae. On the strength of these and of other weighty arguments, in our opinion — strange as it may sound — *Chara* ought to be definitely removed from the fresh water filamentous algae and should be rated as a class of the same rank as *Bryophyta*, as a class in which the gametophytes are much more developed than the sporophytes, with reproductive organs much more developed than those of the filamentous green algae and essentially similar to those of the Mosses *(antheridia* and *archeogonia* or *oogonia)*. In view of these important characters the objection dwindles away that the sporophyte of the *Characeae* as againts the huge gametophyte is shrivelling into a unique cell, the zygote. When taking only this feature into consideration *Chara* really ought to be relegated in the green algae with cell filaments. The multicellular cell-bodied gametophyte and the structure of the highly developed multicellular *antheridia* and *oogonia* are, however, much more comparable with the similar organs of *Hepaticae* and *Musci* than to the

reproductive organs of the fresh water algae with cell filaments. There is a great similarity, however, not only in this respect but also as to the distribution of the reproductive organs, viz. with the monoecism, dioecism and heteromorphous alternation of generations in Mosses.

Summarizing the above statements on the distribution of the reproductive organs, we want to make it clear that the same conditions occur here as in the unicellular organisms. To isogamy corresponds the *isospore*, to homogamy the *homospore* and to anisogamy the *anisospore* or essentially heterospore respectively. Another important finding is that *Musci* and *Hepaticae* are on the same developmental level, since both are Bryophytes and in both the isosporous, homosporous and anisosporous conditions equally occur. The *Musci*, however, exhibit monopodial, while *Hepaticae* more frequently dichotomous branching. Since these two kinds of branching can not be derived from each other, we may draw the same inference as we did in the case of the unicellular organisms and of the Algae, namely that also Bryophytes, similarly to the organisms dealt with hitherto, are of polyphyletic origin. All these grades of the history of evolution were attained by the flora in the palaeszoic age of the Earth, in the Silur, i. e. in the Ordovicium or Gotlandicum, about 400 million years ago.

Stage VII. Psilophyta

As a consequence of the adaptation of the vegetable kingdom to terrestrial life the moss stage made a further progress. The sporophyton phase hitherto vegetatively or physiologically not independent from the air, from the top of the gametophyton gradually came into contact with land, started a more intensive growth and became now able to lead an independent life at the

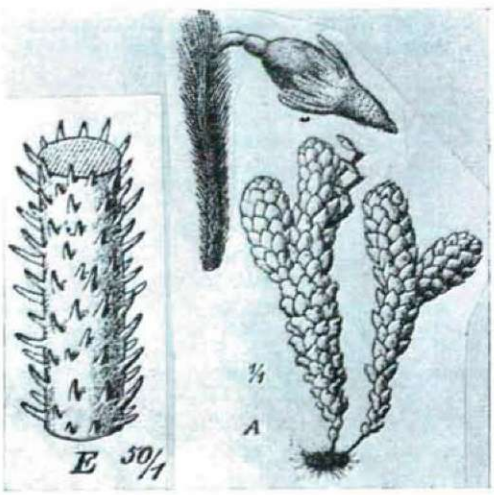


Fig. 17. On the sporophyte of *Eriopus cristatus* there are assimilating *paraphylla* promoting its physiologically independent life. From the surface of the sporophyte of *Lepidopilum subsubulatum* similar epidermal structures, emergencies arise as from the surface of the stem.

expense of the gametophyte. One of the results of this process was that in the hitherto non-branching sporophytic generation tiny assimilating leaves *(microphylla)* developed from which some, particularly towards the apices of the little stems, contributed to the origin of the *sporangia.* This is how on the vascular plants gradually the *sporangium* and *sporophyllum* stage developed.

This developmental stage is seen to materialize among the *Musci,* e. g. in the Australian species *Eriopus cristatus* on the sporophyte of which assimilating *microphylla (paraphylla)* developed, while from the base of the sporophyte root hairs originated (2 n!) or in the fossile primitive shrubs *Psilophyta* and their progeny the *Pteridophyta.* Already the ancient primitive skrubs the Psilophytes of the Cambrian and Silurian to all probability carried isospores or homospores respectively, whose *sporangia* developed partly on leaves, on the so-called *sporophylla* or were located on the top of the leafless stem or at its side in the axil of tiny leaves. We refer to probability, because the Psilophytes are not sufficiently known, so that it is open to discussion whether their sexual generations were monoecious or dioecious. There is no doubt, however, that they must have existed, since their spores are known, and from these only haploid monoecious or dioecious *prothallia* could have developed. According to recent investigations the rhizometype part of *Asteroxylon, Rhynia* in the earth as a matter of fact does not belong to the sporophyte sector but to formallity alike the gametophytic generation and could have presented an analogy to the homomorphous development of *Cladophora* referred to in connection with the Algae. What so ever the *prothallia were,* among the sporophytes (2 n) similarly to the previous findings 3 main types of branching can be distinguished, namely the *monopodial (Rhynia, Hornea),* the *dichotomous (Protopteridium)* and the verticillate (whorled branching (*Calamophyton,* Fig. 18). So in this period again the identical developmental

Stage VII. PSILOPHYTA

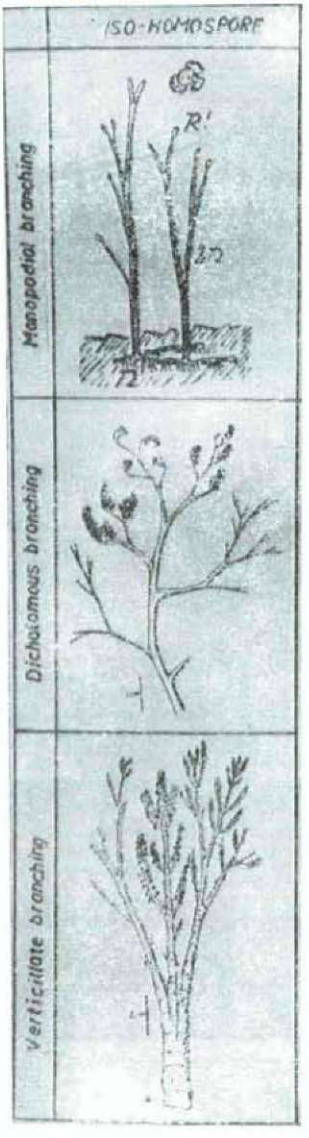


Fig. 18. The gametophyte (n) and sporophyte (2n) of the monopodially branching *Rhynia* are more or less of the same form. The gametophyte might have developed from isospore or homospore. (1) The sporophyte of the dichotomously branching *Protopteridium* must have developed similarly from isospore or homospore. (2) The sporophyte of *Calamophyton* of the verticillate type of branching too are derived from isospores or homospores. Again identical developmental stage and 3 types of branching side by side.

stage of the spores and simultaneously the three forms of branching appear at the same time. The terrestrian flora reached this developmental degree in the history of Earth in the Devonian, the recent representatives of which evolutionary stage are *Psilotum* and *Tmesipteris.*

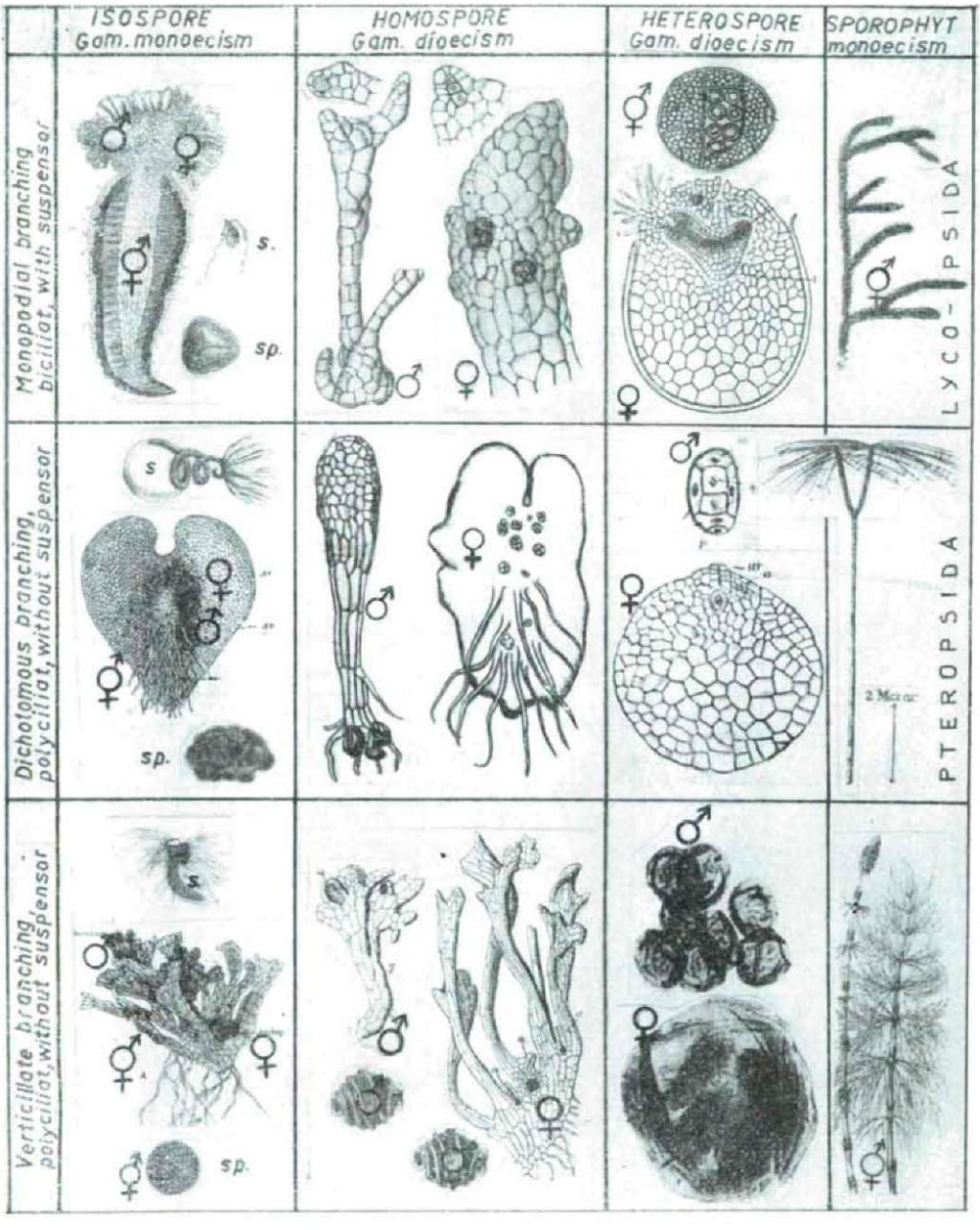
Stage VIII. Pteridophyta

Isosporophylla. Among the Pteridophytes in the strict sense of the term evolution advances further, since at on the macrophyll beneath of the sporophyte *(Filicinae)* or in the *sporangia* of the microphyllous sporophyte *isospores (Lycopodium)* or in the somewhat more developed form of the latter homospores *(Equisetum)* develop, while in others in the same *sporangium* already micro- and macrospores, i. e. heterospores *(Marsilea)* and finally in the most developed stage on the monoecious or dioecious sporophyte in the differentiated *microsporangia* only microspores and in the *macrosporangia* only macrospores formed *(Selaginella)* and either in one common or separate so-called (macro-sporophyllous or microsporophyllous *strobiles.*

Where do these stages of sexual differentiation, the *isospores, homospores* and *heterospores* appear within the *Pteridophytes?* The *Pteridophytes* are ranged in three great classes: *Lycopsida, Pteropsida* and *Sphenopsida.* To *Lycopsida* belong the *Lycopodia* and *Selaginellae,* to *Pteropsida* the *Filicinae, Hydropterides* and *Isoetales,* while to *Sphenopsida the Equisetum* sp. and the fossile *Chalamites.* The stem branching of the microphyllous *Lycopsida* is generally monopodial, while the terminal branchings of the conductive bundles and ribs of the macrophyllous *Pteropsida* are nearly always dichotomous and the *Sphenopsida* exhibit a typical verticillate branching. A study of these three

Fig. 19. Monoecism-dioecism and heteromorphous dioecism in the *prothallia* of the *Pteridophyta (Lycopsida, Pteropsida, Sphenopsida).*
1. From the isospore of the microphyllous *Lycopodium clavatum* of the monopodial type of branching a monoecious *prothallium* originates.
2. From the homospore of *Lycopodium sp* a female-type macrospothallium and a male-type microprothallium of smaler size develops.
3. From the microspore of the similarly monopodially branching microphyllous *Selaginella* male-type, while from the macrospore female-type *prothallia* develop (heteromorphous dioecism).
2. row. From the isospore of the macrophyllous *Dryopteris filix mas* a monoecious *prothallium* originates, while from the homospore of *Ceratopteris thalyctroides* a dichotomously branching female-type *macroprothallium* and a male-type *microprothallium* of smaller size develop. The spores are morphologically analogous but physiologically different, i. e. homospores. From the microspore of the polyciliate *Isoetes lacustris* a maletype *microprothallium,* whereas from the macrospore a much more developed female-type *macroprothallium* develops.
3. row. From the isospore of *Equisetum* only one bisexuell sort of *prothallium* (after SCHMIDT) from the homospore of *Equisetum arvense* fifty per cent female-type and fifty per cent male-type *prothallia* originate. From the macrospores of *Paracalamostachys striatus* of the Carboniferous, a plant of verticillate branching, female type *prothallia* originated, while from the microspores male-type *prothallia.* The upper row is characterized beside the spore types by monopodial branching, biciliate spermatozoid and a suspensor on the embryo. All these properties are phylic features and seem to evidence that the three phyla *Lycopsida, Pteropsida* and *Sphenopsida* developed independently from each other and concurrently until the heterosporous stage.

Stage VIII. PTERIDOPHYTA



main types as to the location of their spores and reproductive organs in general reveals that in all three types the isosporous, homosporous and heterosporous developmental stages exist. But the same conditions were found in the characteristic forms of the Carboniferous, namely in the monopodially branching *Lepidodendron,* in the dichotomously branching *Sigillaria* and in the verticillately branching *Calamites.*

Thus within the *Pteridophytes* again the same developmental stages, sexual differentiations and the three main types of branching appear as in the unicellular organisms, the *Algae, Mosses* and primitive shrubs: namely the gametophytes of the *Pteridophyta* too are either monoecious or dioecious, while the sporophytes are still exclusively monoecious.

In recent ferns e. g. in *Selaginella* the sexual conditions are probably much the same as in the Lepidodendrous which liver in the Carboniferous. Both spores of *Selaginella* from the same strobile drop at ripening to the earth where fertilization can take place only through water as a medium. Inspite of the high degree of differentiation in the flora of the Carboniferous sexual propagation was still linked with the temporary presence of liquid water. In the phylogeny of the vegetable kingdom and particularly in the development of terrestrial vegetation it was the most important period when the vegetable kingdom made itself independent from the presence of liquid water at fertilization; this developmental stage had set on in the Carboniferous. According to our present knowledge in the Carboniferous both the macro- and microspores

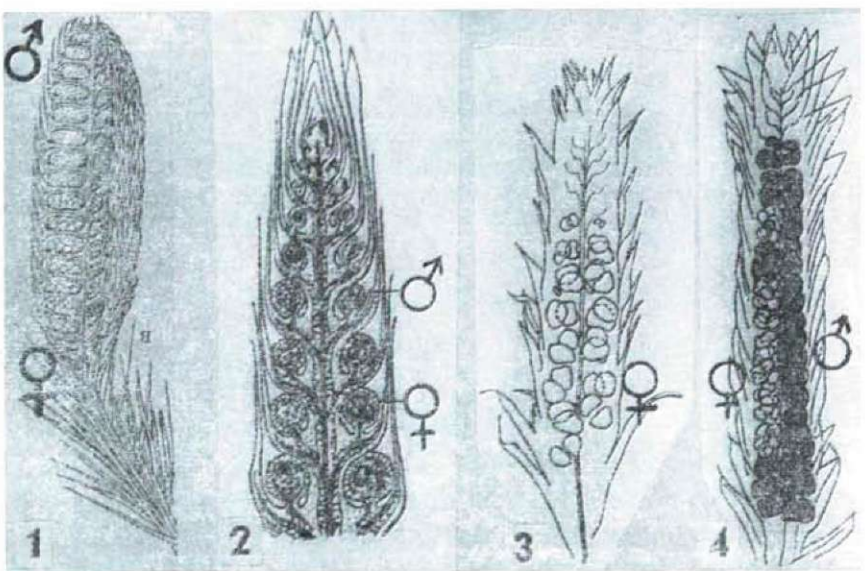


Fig. 20. In the sporophyllic string of *Lepidodendron* below in the *macrosporangia* the macrospores and in the *microsporangia* the microspores are localized. This strobile structure points to monoecism. (1) Exactly the same structure is found in recent monoecious *Selaginellae* (2) or in the strobile of the fossile *Calamites* which are of the same age the *Lepidendrons.* In the strobile of *Selaginella* sp. are only macrosporangia localized (3), on other *Selaginella* species the macro-and microsporangia non separately one above the other, but side by side are localized. (4).

from the strobiles of *Sigillariae Lepidodendrons* and *Calamites* still roppen to the earth, possible on banks, where they germinated, and fertilization also took place on the earth through the medium of liquid water. The embryo which came into being after fertilization continued its development on the earth, as a rule in a moist environment.

Stage IX. Pteridospermae

Isospermia, Homospermia. The change of this stage was marked by the phenomenon, that the *macrosporangia* did no more drop on the earth, on the banks, but remained connected with the mother plant until the fertilizing sexual cells (microspores) were carried no more by the water but by the wind within easy reach of the *macrosporangia*. Thus the act of fertilization has been again raised into the air, on the sporophyte, where the role of the water has been now taken over by the wind. The result of fertilization on the sporophytic mother plant in the air became a new structure, the *seed*, which dropped to the earth only after nutrition by the sporophytic mother plant and a certain development, and which organ now already represented all properties of both parents, the same as the zygotes of the unicellular organisms or of the multicellular algae or the sporophytes of the *Pteridophyta*.

Stage IX. PTERIDOSPERMAE

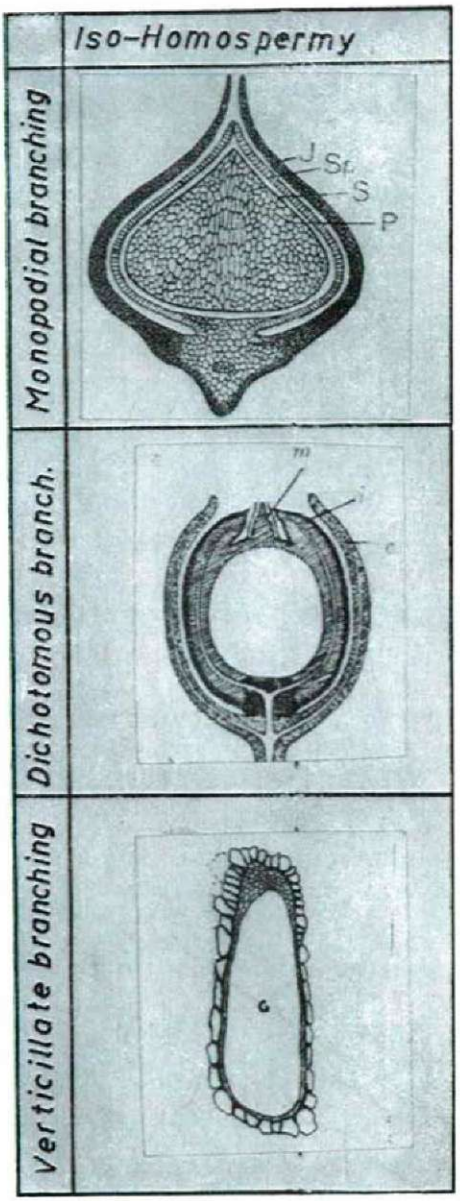


Fig. 21. 1. The structure of the ovule in *Lepidocarpon lomaxii* (microphyllous type). To all probability it has been monoecious.
2. The open ovule of *Lyginodendron Oldhamium. (Pterispermae).* (The mother plant was probably dioecious.)
3. The macrospore of the recently discovered verticillate *Calamocarpon insignis* (BAXTER) and in it the gametophyton (G). All three are *Pteridospermae* and represent the three main branching types on the identical degree of development.

Since in these primitive *Pteridospermae* in separate *sporangia* microspores and distinct macrospores developed which might have developed separately but also in the same strobile, so the sporophytes were monoecious, but they might have also developed in different strobiles and either on the same individual when they are monoecious (Fig. 22) or on different individuals when the sporophytic generations became dioecious. With this further step the sexual dimorphism now extended from the gametophyt to the sporophytic generation, and so gradually monoecious and dioecious terrestrial Spermatophytes began to develop. In the history of evolution of the vegetable kingdom, this high degree of morphological sexual dimorphism obtained a decisive importance in the conquest of the mainland, because the sporopherous vascular plants gradually began to develop into Spermatophytes. No essential change occurred in the mutual relationship of the two sexes, because the primitive Spermatophytes also continued to be either monoecious or dioecious.

According to our present knowledge the development of seed materialized within the Pteridospermae at least in three directions *(Lyginodendron, Lepidocarpon* and *Calamocarpon)* (See Fig. 21.) why the seedlike megasporangia of the verticillate branching is discouvered recently by BAXTER. The realization of this evolutionary degan about 320 million years ago in the Carboniferous.

Stage X. Gymnospermae

The further transformation of high importance was initiated by the condition that the *macrosporangia* of female character in the aments and on the *macrosporophylla* remained free for the time being and thus were exposed to rather manyfold dangers. Gradually the *integument* enclosing the *macrosporangium* (Fig.) began to provide for their protection, but the *macrosporangia* did no more drop on the ground for the period of fertilization where hitherto the liquid water was the medium of fertilization. This intermediary role has been assumed now in the air by the wind. Since these primitive ovules developed from the *macrosporangia* when they were still free, the seeds which came into being after fertilization also remained open. This is how the first Gymnosperms came into existence. Let us see, by what means?

The formation of Spermatophytes.

It has been shown on the recent *Selaginellae* and on the fossile Lepidodendrons that in the same strobile there are or were both *micro-* and *macrosporangia* together. From this sporous condition the gymnospermous condition could have come into existence by means of development in some individuals in the individual mixed strobiles gradually either into macrosporophyllous strobiles only, while in others to microsporophyllous, strobiles or aments only. Thus the mixed strobiles gradually began to transform into unisexual ones and by this phase the sexual dimorphism extended to the strobiles. Such primtive condition occurs even today in some individuals of recent *Selaginellae (Selaginella apus* et c.) but, to all probalility, the same thing happened with the most developed ferns of the Carboniferous, the *Lepidodendrous* or *Pteridо-*

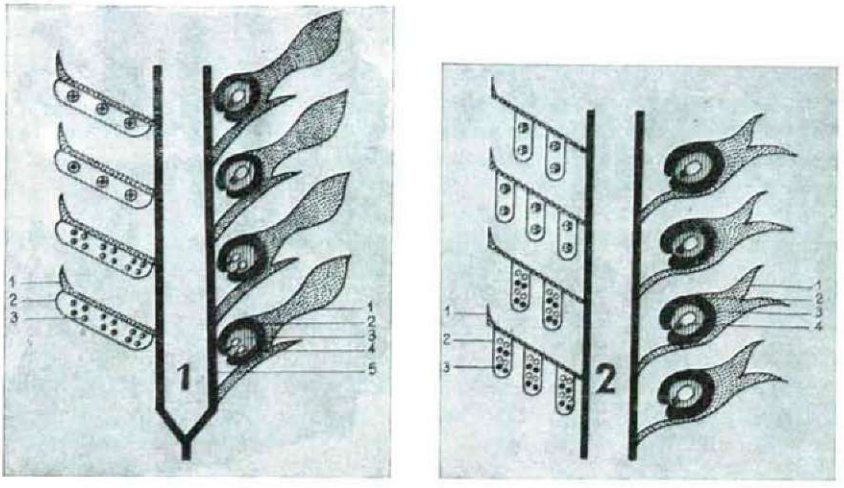


Fig. 22. Distribution and structure of the strobiles of the monoecious (isospermy) and (homospermy) dioecious Gymnosperms.

spermae. Since both sexual characters were inherent in the sporophytic generation, the segregation of sexuality extended either to some branches of the same individual and hereby the monoecious gymnospermous Spermatophytes came into existence, or one of the sexual character depressed the other so far that only that one could assert itself particularly, namely the male or the female character only, and as a result two kinds of sporophytous Spermatophytes, i. e. dioecious plants came into existence. The other sexual character did not cease to exist in these plants entirely because it continued in latent state in the apparently unisexual sporophyte. This is why in the male individuals of some dioecious Spermatophytes female characters, while on the female individuals male characters could appear, e. g. in some aments of Gymnospermous plants carpels develop and vice versa *Pinus)*.

Isospermy, homospermy. Sporophyllum strings, aments, strobiles, dioecious and monoecious spermatophytous condition.

After the monoecious and dioecious ferny stage only the gymnospermous spermatophytous could have succeeded, either in the monoecious or in the dioecious form. Monoecism and dioecism are both spermatophytous conditions though among the Gymnosperms, but there are very essential physiological differences between the seeds because tho one kind of seed produces only one kind of individual, namely a monoecious plant, a sporophyte, while the other develops two separate individuals, sporophytes i. e. dioecious plants. In the unicellular organisms, in filamentous Algae, in Mosses and in the Pteridophytes too, we observed that from the isospores only one kind and from the homospores (zygotes) two kinds, namely individuals, gametophytes of male and female character develop. Exactly the same conditions continued to prevail also in the monoecious and dioecious gymnospermous Spermatophytes. In

these no several different cases can occur either. Therefore on account of the analogy or identity with the previous forms we may term the seeds of the monoecious Gymnosperms as isogymnosperms and those of the physiologically different dioecious as homogymnosperms, since from the point of view of sexuality there is the same cytological i. e. heterochromosomatical difference among them as among the isogametes, isozygotes, isospores and among the homogametes, homozygotes and homospores. Here, as in all other cases, the sexual differences are caused by the heterochromosomes as invariably evidenced beyond doubt by cytological examination. This might also explain the fact that e. g. in some dioecious *Cycadales* the chromosome number is 8 or 9, depending on whether male or female individuals were examined and which specimen was heterozygotic. In this connection the question arises by what means these monoecious and dioecious conditions i. e. *isospermy* and *homospermy* materialized in recent and fossile *Gymnospermae* and *Chlamydospermae*. These gymnospermous Spermatophytes are also either monoecious or dioecious, but several types may be distinguished among recent and fossile Gymnosperms. The dioecious *Ginkgoales* and *Cycadales* belong here, but can be relegated to them. A closer examination of these forms reveals three main types of branching in the stems, branches and in the terminal branching of the conductive bundles of the ribs, namely among the monoecious *Coniferae* in the strict sense of the term the monopodial, among the dioecious *Cycadales, Ginkgo, Araucariae* and *Podocarpus* in the leaves dichotomous, and the mono- and dioecious *Cupressaceae* the opposite or verticillate branching.

Stage XI. Chlamydospermae

Similarly in the dioecious *Chlamydospermae* (Fig. 24), *Gnetum* represents the monopodial, *Welwitschia* the dichotomous (parallel) and *Ephedra* the whorled type of branching so that within the gymnospermous condition again the same developmental stages appear in each phylum which seems to indicate that the *Chlamydospermae* are not of homogeneous origin either; there is no doubt that they have reaced the gymnospermous state in the monoecious or dioecious form, proceeding from several types. Thus their origin is, similarly to the previous types, polyphyletic.

Stage XII. Angiospermae

The gradual evolution did not stop at the gymnospermous condition reached in the Carboniferous and Permian systems. Beginning from these periods gradually a new developmental stage materialized in the life of the vegetable kingdom. This transformation presents a change in the sexual reproduction pattern of the plants, substantiating at the same time the great adaptability of plants to the prevailing environmental conditions. This change became manifest in the first place by the phenomenon that the free *macrosporangia*, the so-called *ovules*, which on the *macrosporophylla* were covered by a thin integument, became now gradually covered by the edges of the sporophyllums. Hereby a completely new so-called *angiospermous* developmental stage arose,

Stage X. GYMNOSPERMAE

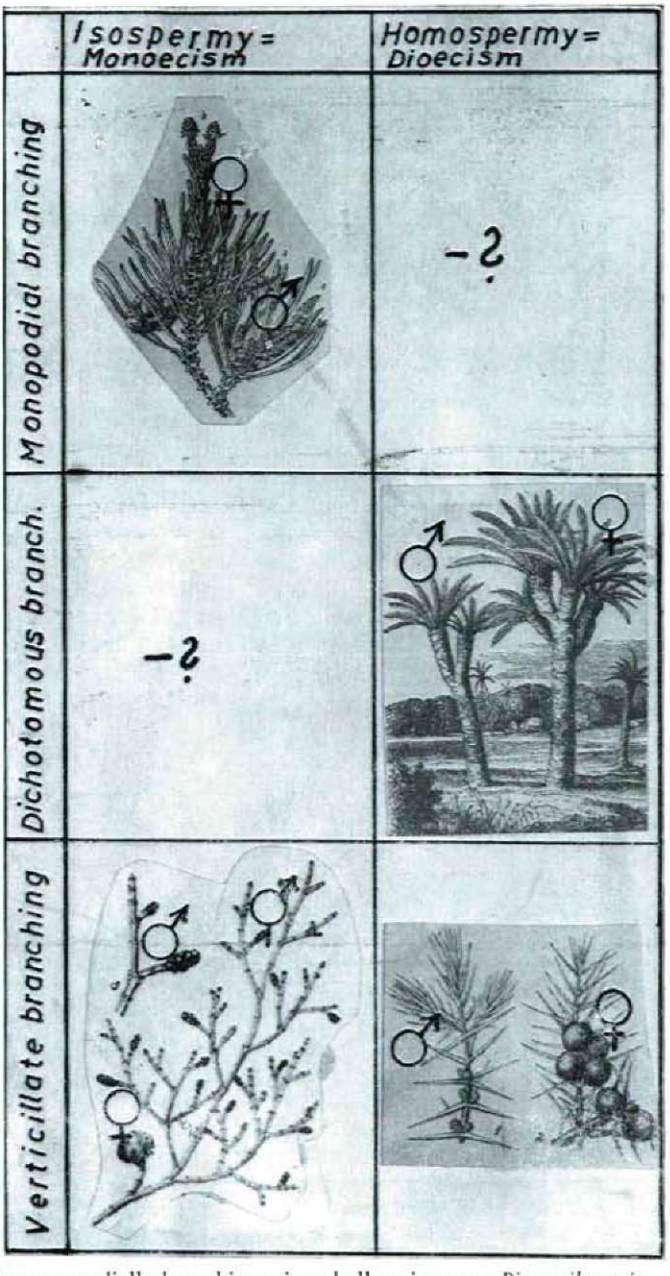


Fig. 23. 1. The monopodially branching microphyllous isosperm *Pinus silvestris.*
3. The verticillately branching of the isosperm *Tetraclinis articulata,* and of the homosperm *Juniperus communis.*
2. The macrophyllous dichotomously branching *Cycas revoluta.*
All three are Gymnosperms, but of three different types of branching.

Stage XI. CHLAMYDOSPERMAE

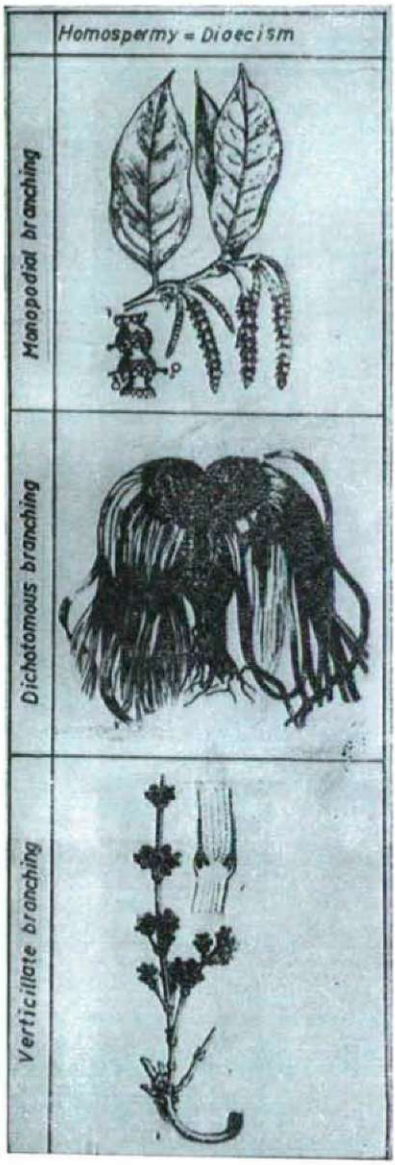


Fig. 24. 1. Gnetales, 2. Welwitschiales, 3. Ephedrales

when the so-called *carpel* entirely enclosed the thinly wrapped *macrosporangia*, the ovules, and thus the female reproductive organ assuring the survival of the species got into a completely protected position.

So from the *macrosporophyllum* gradually the pistil developed, the parts of which are the *ovary*, the *style* and the *stigma*. In this closed condition and high in the air even the temporary presence of liquid water became superfluous. By degrees the plants could do even without the wind, because from the early tertiary period the microspores (pollen grains) could be and were actually transported by the then widespread insects to the *macrosporophylla* of female character, to the pistils and in the first place to the primitive stigmas.

But even this did not happen at once, because this development had its degrees, too. What were these degrees? Similarly to the previous developmental stages also among the recent Angiosperms both monoecism and dioecism occur, but besides an entirely new form, the hermaphrodite or monoclinous flower makes its appearance. On separate branches of the same individual of the monoecious angispermous plants the strobiles of different sex, male aments and female flowers appear. Similarly to the cytological analogy of isogamy, isozygotes and isospores and to the term isosperm of Gymnosperms the seeds of the monoecious Angiosperms are named isosperm. On certain individuals of other species again we find only a male aments, while on other individuals exclusively female flowers. Such dioecious angiospermous Spermatophytes on the analogy of homogamy, homozgygote, homospore, homospermy might be named homosperms. Finally, from Angiosperms a particularly large number had reached the condition where in the same structure the reproductive organs representing both sexes are present together, i. e. both the *microsporophylla* which in this new structure are already termed *stamina*, and the *macrosporophylla* or pistils. At last, in the course of an evolution spanning thousand millions of years, the reproductive organs representing both sexes, the whole sexual generation, came close together on a single

sporophytic individual and within a single structure, the monoclinous flower. In the seeds of Angiosperms developing such monoclinous or hermaphrodite flowers the chromosome set of the cells, or at least the compounds involved in the formation of sexuality are present in another configuration than in the monoecious (isospermic) or dioecious (homospermic) plants and therefore, to distinguish them from the first two, they may be termed eusperms. Accordingly, the hermaphrodite condition of the sporophyte is the most developed stage reached by the plants starting from the unicellular condition during a development of many hundred million years, the forms of which we now encounter at all times and in all places. The hermaphrodite flower is, consequently, the highest stage in the history of evolution of the vegetable kingdom and it only could have developed according to the author's opinion — as demonstrated — from the unisexual strobiles. Let us examine, by what means this has been accomplished.

The origin of the hermaphrodite flower

This question is up to our days one of the most contested problems of the philogeny of plants. In our opinion, this latest monoclinous hermaphrodite condition could have developed only from the previous stages and from the unisexual flowers, because there was no other possibility in the Permian, Triassic and Jurassic periods. But even before, only two cases were possible, since among the primtive gymnosperms too only the monoecious and dioecious conditions existed so that only these could have been transformed into hermaphrodite flowers. But by what means? In our opinion, either by the development of *microsporophylla (stamina)* in the pistillate, i. e. macrophyllous strobilaceous flowers on the place of part of the carpels, e. g. at the bottom of the strobiles (pistils), by thrusting into the background the compounds eliciting female character. Thus the *stamina* and the pistils got next to each other and hereby became hermaphrodite flowers; or in the aments, e. g. on their top

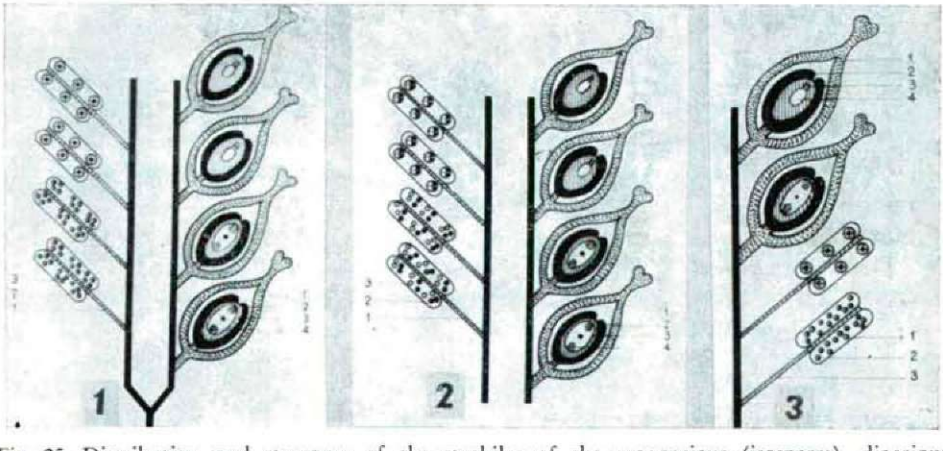


Fig. 25. Distribution and structure of the strobiles of the monoecious (isosperm), dioecious (homosperm) and monoclinous (eusperm) Angiosperms.

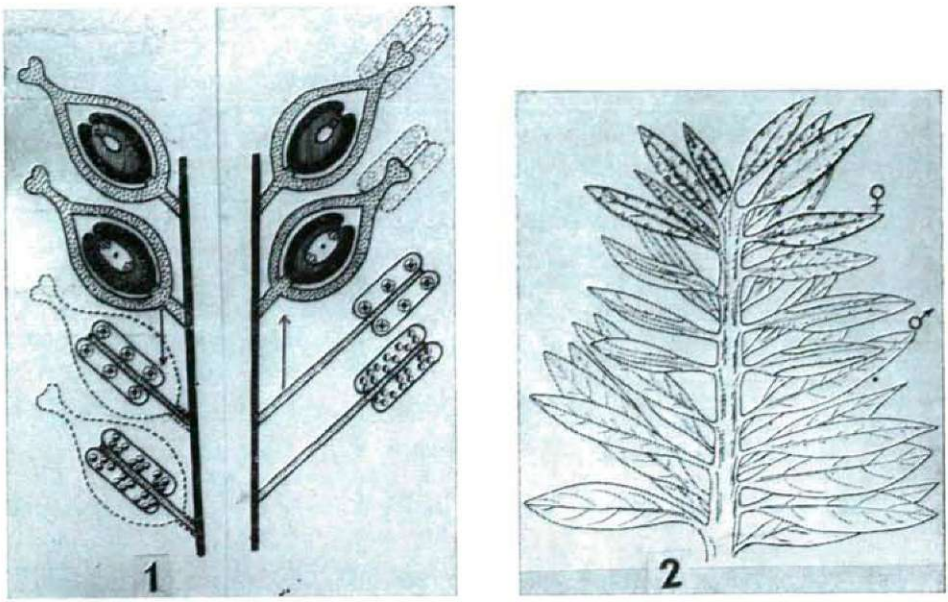


Fig. 26. The origin of the hermaphrodite flower. 2. Proangiosperm flower after *Hutchinson*. From under, upwards foliage leaws, after microsporophylla and macrosporophylla.

mainly pistillate flowers (pistils) came into being and this way the organs representing the two sexes got again next to each other and this could have been also a pattern for hermaphrodite flowers to develop. This process might have originated both in monoecious and dioecious gymnosperms, the more, since all sporophytes are essentially always hermaphrodite individuals in which the chromosomes and compounds determining the two sexes only separate from each other when partly the aments *(stamina)* and partly the carpels (pistils) originated. The probability of this assumption is enhanced by the fact that a similar phenomenon can be observed even in our days both in Gymnosperms and in Angiosperms. In the catkin of the willow tree e. g. frequently pistils occur among the *stamina* which shows that organs representing the two sexes can develop in the same structure quite close to each other and this way true hermaphrodite flowers come into being (androgynous aments). The same phenomenon can be observed, however, as an extraordinary occurrence, in maize, where from the middle of the tassel a pistiline strobile emerges with genuine ovules and seeds respectively. Similar phenomena are encountered in Gymnosperms *(Pinus)*.

In our opinion this process presents essentially the same general biological regularities which were observed hitherto in all developmental stages. The reproductive organs of our simplest monoecious and dioecious herbaceous Angiosperms invariably concentrated in monosexual strobiles similar to those of the Gymnosperms and particularly in male and female aments or coniform structures respectively. In the strobiles of both pheno- and genotypes always

the character representing the other sex, so both components of DNA were also present, but one of the component in latent condition, in the staminate aments the character determining the female sex and in the pistillate ament the character representing the male sex and the DNA respectively. Only upon the external and internal factors, so upon the contrasting configuration of DNA or upon the effect of the different hormones in one of the phenotypes one of the sexual characters appears while the other remains in recessive and latent condition as if in an expectant attitude. The development of the monoclinous flower must have started, in our opinion, always from such latent hermaphrodite condition, in a way that within the unisexual strobile, e. g. in the staminate ament, which may be considered essentially as an overmale individual, the female character hitherto depressed and in a latent, recessive condition, could have — as a result of the diminution of the male character — got gradually in a dominant position towards the apex of the ament. As a consequence the place of the upper *stamina* has been gradually more and more occupied by the female character — as one half of the intersex — that became more and more definite, while at the bottom of the strobile the old *stamina* continued to represent the male genotype. As a contrast in the pistillate ament that may be considered as overfemale, the male character, hitherto in latent condition, began in the bottom of the ament to transform also in its phenotype into stamina, i. e. to become dominant, so that in the final result the ament developed into a hermaphrodite flower. Essentially the same phenomenon is manifest here which has been demonstrated in the unicellular *Chlamydomonas eugametos*, when the unisexual individuals could be transformed by the influence of chemicals into individuals of the other sex.

This concept essentially agrees with the Euanthium theory according to which in the hermaphrodite flower the *stamina* should not be regarded as staminate flowers but as *microsporophylla* and the pistils not as female flowers but as *macrosporophylla.*

So within the Angiosperms we can distinguish monoecious, dioecious and hermaphrodite flowered individuals and these differences can be traced back to the different nature of the seeds, more exactly to factors determining sexuality.

It remains to examine how these developmental stages become manifest in the Angiosperms. The Angiosperms are divided in two great classes: *Monocotyledones* and *Dicotyledones*, both of which contain plants with monoecious, dioecious and hermaphrodite flowers. In the *Dicotyledones* monoecious, i. e. isospermic plants are e. g. the *Amentiflorae*, dioecious e. g. the *Salicaceae* and hermaphrodite generally the *Dialipetalae*. From the *Monocotyledones* e. g. the *Caricoideae* and *Palmae* are monoecious, the *Palmae* dioecious and the *Liliaceae* hermaphrodite.

As regards branching dicotyledons generally exhibit monopodial branching while monocotyledons — when taking into consideration the parallel nervure and also the branching of the stems in *Palmae, Dracaenoideae, Cordyline* etc. — rather more dichotomous. Finally when reallocating *Casuarina* to the Angiosperms, we will find also the third (whorled) type of branching represented. The essence is, however, that both in *Monocotyledones* and in *Dicotyledones* the same developmental stages, monoecism, dioecism and hermaphro-

Stage XI. ANGIOSPERMAE

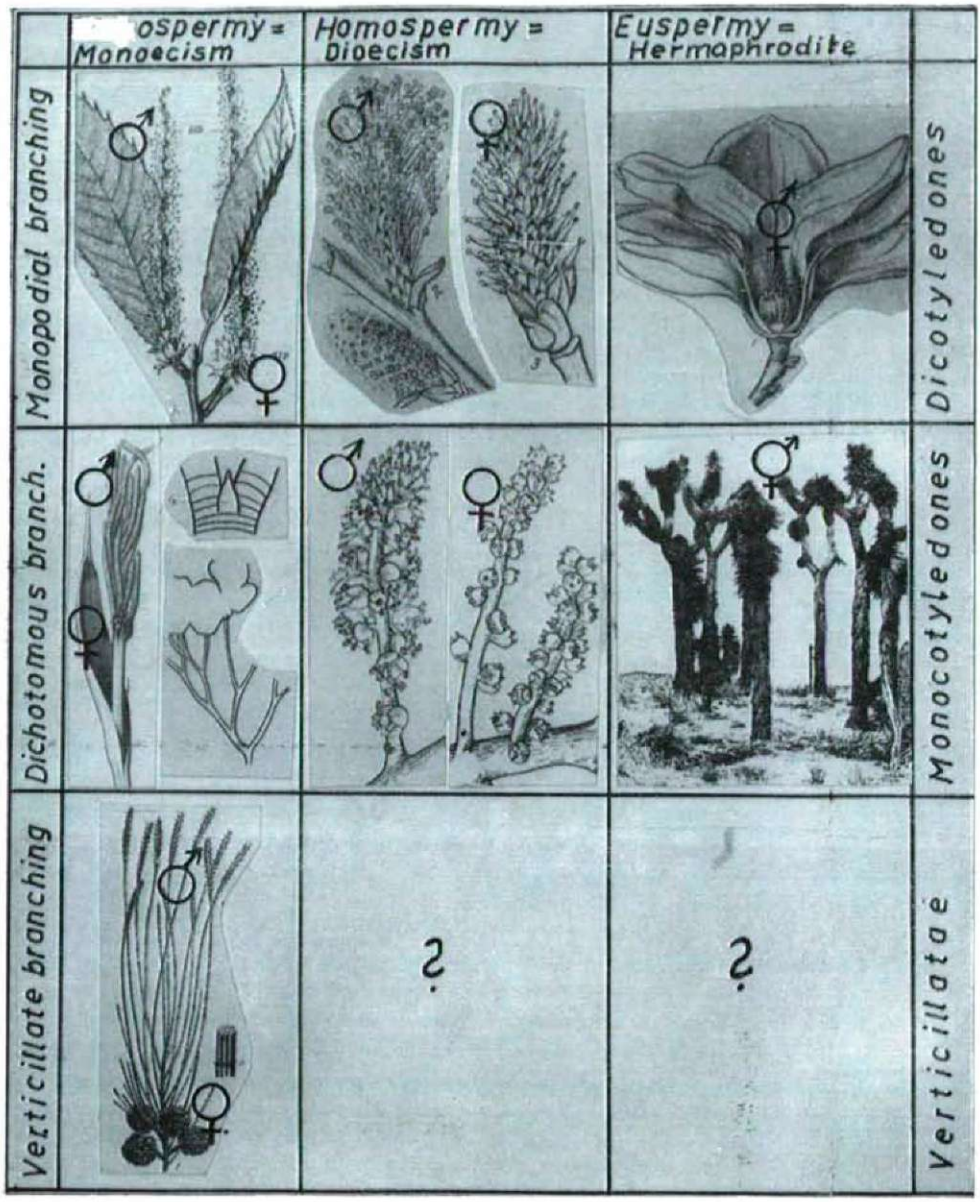


Fig. 27. The dicotyledonous and monoecious *(isosperm) Castanea sativa* of monopodial branching. The flower of dioecious *(homosperm) Salix caprea* and of the *(eusperm) Magnolia acuminata*.
2. The palm of dichotomous branching *(isosperm)*, the dioecious *homosperm* palm with dichotomous branching and the hermaphrodite *Yucca arborescens* of dichotomous branching.
3. The monoecious *(isosperm) Casuarina verticillata* of verticillate branching.
All three series are in the developmental stage of *Angiospermae*, but with three different types of branching.

ditism occur. In our opinion, the monoecism or dioecism of the *Monocotyledones* could not have developed from the monoecious or dioecious stage of *Dicotyledones* neither the hermaphrodite condition of the *Monocotyledones* from the analogous condition in the *Dicotyledones;* these derive, to all probability, from the *Bennettites,* which seems to evidence that the origin of monocotyledons is independent of the origin of dicotyledons. Consequently the *Angiospermae* do not originate from a single common phylum, but at least from two or three phyla substantially differring from each other, and according to the athor's opinion so they are of polyphyletic origin.

Summary

1. Phylogenetic stages. As established in the previous chapters and in accordance with the present state of science, in the history of evolution of the vegetable kingdom the terrestrial plant from their beginnings in the inorganic wordl during their development in the course of 2 to 4 thousand million years passed through the following stages:

Stage I. Beginning of the + and — contrast among the inorganic compounds and their transformation into living compounds.

Stage II. **Virophyta.** Physiological differentiation of the + and — character in the simplest forms of life at the boundary of the inorganic and organic worlds.

Stage III. **Bacteria and Cyanophyceae.** Simplest uni or pluricellular plants without a definite cell nucleus, with + and — sexuality and concealed alternation of generations.

Stage IV. **Monadophyta.** Unicellular plants with definite cell *nucleus,* living both in water and on land, with definite + and — sexuality and alternation of generations.

Stage V. **Algophyta.** Unicellular cell-filamentous, cell-lamellar, cell-bodied plants living both in water and on land, with definite + and — sexuality and alternation of generations, where the gametophyte is multicellular, the sporophyte unicellular or homomorphous with the gametophyte.

Stage VI. **Bryophyta.** Sexually differentiated cormophyt plants, living in water but mainly on land, in which the multicellular gametophyte is physiologically independent and more developed than the equally multicellular sporophyte. The sporophyte has no contact with the soil and is nourished by the gametophyte.

Stage VII. **Psilophyta.** Partly extinct (fossile) terrestrial or aquatic sporipherous plants where the gametophyte and the sporophyte were about equally developed.

Stage VIII. **Pteridophyta.** Terrestrial or aquatic sporipherous plants in which the sporophyte is physiologically independent and much more developed than the physiologically equally independent gametophyte. Both the sporophyte and the gametophyte are in contact with the soil or with the water.

Stage IX. **Pteridospermae.** Extinct (fossile) terrestrial plants which in their exterior are suggestive of the *Pteridophyta*, where the gametophyte of both sexes has developed on the sporophytic mother plant, the female gametophyte had been covered by a thinner or thicker integument and which after fertilization had developed to seed. The medium between the two sexes is probably still the water.

Stage X. **Gymnospermae.** Terrestrial plants in which the enclosed female gametophytes develop as open structures on the strongly developed sporophyte. The unicellular male gametophytes, independently from the liquid water, through the intermediary of the liquid water, through the intermediary of the wind and of the pollen tube get near the female gametophytes while from the seeds originating from the fertilized female gametophytes monoecious and dioecious individuals, sporophytes arise.

Stage XI. **Chlamydospermae.** Spermatophytes in which the female gametophyte is already more cut off from the environment; the male gametophytes come to get near the female gametophyte by the intermediary of the wind, exceptionally of insect or the pollen tube respectively. From the fertilized female gametophyte such seeds develop on the female sporophyte which give rise to dioecious sporophytic individuals only.

Stage XII. **Angiospermae.** Terrestrial spermatophytes in which the female gametophyte is already completely cut off the immediate environment and the fusion with the male gametophyte at fertilization can only take place by the pollen tube. The seeds developing from the fertilized gametophyte give rise to sporophytes with monoecious dioecious or hermaphrodite (monoclinous) flowers.

As demonstrated above, each phylogenetic stage is characterized by properties involving distinct differences from all other developmental stages before or behind it and which differences evolved from each other during many million years from the similar previous forms.

Probably no research worker has or could have any doubt about the natural stages listed, therefore these findings can be taken as basis for further investigation.

2. Sexuality is an objective natural law.

It is an universal law of nature that the individuals of living beings, unicellulars as well as the most developed phanerogams, in their vital processes besides the instinct of self preservation have been and are directed always by the instinct of race preservation, of sexuality, of + and —, male and female character and that the substances carrying the determination of sexuality (gametes) are manifesting themselves most conspicuousli in the sexual organs and in their appearance respectively. Without sexuality and development of sexual organs the gradual evolution of the vegetable kingdom through thousand million years can not be conceived. Sexuality is not an occasional morphological

property but a character phylogenetically fixed in the species, a fundamental principle, a natural law under the cogent influence of which the whole living world stood from the very beginning and still stands in our days.

3. Monoecism and dioecism are objective laws of nature.

With the above fundamental law by necessity an other biological law is linked according to which in the sexual processes the evolution of the species and the formation of new species is furthered in the first place by heterofertilization. This principle materialized in the vegetable kingdom by different means. Its simplest way is seen in the unicellular organism where within the species individuals of opposite sex, monoecious or dioecious come into existence. If on the other hand the individuals are multicellular, the sexual cells of different sex develop either in the various cells or organs of the same individual, when the individuals are essentially again monoecious, or the male and female sexual cells, the gametes, develop in the cells or organs respectively of two different individuals, consequently the members of the species sexually, physiologically and morphologically completely separate from each other, thus the individuals are essentially dioecious.

Monoecism or dioecism are in all phylogenetic stages invariably carried by the sexual cells *(gametes)* or the asexually originated cells *(spores)* or by the *seeds* arising from the sexual process in a way that in each phylogenetic stage monoecism or dioecism according to the environmental conditions always appears. Thus monoecism and dioecism form a basic biological law and their immediate causes can be always traced back to contrasting chemical compounds of to cell particles by which they are carried.

In the course of phylogeny monoecism and dioecism materialized in the various developmental stages as follows.

I. *Virophyta*			
II. *Bacteria*			
III. *Cyanophyta*			
IV. *Monadophyta*	*Monoecism*	*Dioecism*	*Dioecism*
(Flagellatae)	Isogamy	Homogamy	Anisogamy
V. *Algophyta*			
(Chlorophyta) (multicellular)	Isozygote	Homozygote	Heteromorphism
VI. *Bryophyta* and *Charophyta*	Isospore	Homospore	Anisozygote ?
VII. *Psilophyta*	Isospore (?)	Homospore (?)	Anisospore?
VIII. *Pteridophyta*	Isospore	Homospore	Heterospore
IX. *Pteridospermae*	Isospermy	Homospermy	(Heterospermy?)
X. *Gymnospermae*	Isospermy	Homospermy	(Euspermy?)
XI. *Chlamydospermae*	—	Homospermy	(Euspermy?)
XII. *Angiospermae*	Isospermy	Homospermy	Euspermy

Accordingly in the various developmental stages monoecism and dioecism from the condition of the unicellular gametes to the Angiosperms always existed and continue to exist in our days.

4. The branching of monoecious and dioecious plants.

Both monoecism and dioecism appear in the various developmental stages never in a single form but invariably in 2 or 3 basic forms of branching. The unicellular organisms exhibited an incredible variety of forms; the main types of branching began to develop from them.

The main types of the branching in multicellular organisms can be traced back in the final result to 3 basic types, the monopodial, dichotomous and verticillate types. These 3 main types of branching were from the multicellular stage of *Algae* to the stage of Angiosperms in all periods closely connected with sexuality and although they underwent some modification in the course of phylogeny still they maintained the ancient character of branching even on the most developed forms until the present day.

Within the individual developmental stages and systematic groups there are so deep differences in branching that it is almost impossible to assume that they might have originated from each other, e. g. *Musci* and *Hepaticae* within the Mosses, and *Lycopsida, Pteropsida* and *Sphenopsida* within the *Pteridophita.*

5. The joint appearance of (1) sexuality, (2) monoecism-dioecism and (3) branching in the various phylogenetic stages.

In the Table which follows, the 3 main forms of sexuality; monoecism, homomorphous and heteromorphus dioecism are established and brought into connection with the systematic categories prevailing in our days and with the three main forms of branching.

If from this survey it can be established that in the course of evolution the individual phylogenetic stages always appeared in the three main types of branching and in the condition of monoecism or dioecism *(isogamy, homogamy, anisogamy, isospore, homospore, anisospore, isosporophyllum, homosporophyllum, heterosporophyllum, isospermy, homospermy* and *euspermy)* so it can be surmised and properly so, that the individual phylogenetic stages in the course of the history of evolution continued or have been modified always in the same type of branching from which they themselves derived. Since these main types of branching, i. e. the monopodial, dichotomous and verticillate types of branching existed from the algal stage to the Angiosperms, and continued to exist to our days, so the assumption is justified that the higher forms of monopodial branching derived from the less developed but also monopodial stages and not from the dichotomous or verticillate. This assumption is also inversely valid, namely these main types of branching did not originate anew in each higher developmental stage and in each subsequent geological period. E. g. all three forms of branching of the Psilophytes of the Devonian or all three forms of branching of the Pteriodophytes of the Carboniferous, or all three types of branching of the Gymnosperms or Angiosperms of the Permian brought both their monoecious and dioecious conditions and types of branching with them from the previous periods, for instance the *Monocotyledones* the dichotomous and the *Dicotyledones* the monopodial branching.

It should be noted by the way that there is no perfectly dichotomously branching dicotyledonous lignous plant nor ever has been; such can occur

only among the Monocotyledons (*Palmae, Yucca, Dracaena* etc.). — Consequently the development must have been from the very beginning and by necessity polyphyletic, because it can be explained only by such polyphyletic development that in the existing systems at the same developmental stage forms of widely different branching could get beside each other the derivation of which from each other is not possible with any effort.

The individual evolutionary phases (I—XII) and within these the types of branching and the distribution of the sexual organs are included in the following combined table in which the author intends to present the evolutional system of the fresh water and terrestrian plants independently of the sea plants. In a separate global table the author presents his triphyletic evolutionary system including the characteristic representants of both fossil and recent fresh-water and terrestrial vegetation according to evolutionary degrees and geological ages. The distribution of the system is as follows.

SUMMARY

Stage I. Inorganic and organic substances + and — compounds.

Stage II. *Virophyta*

+ and — compounds, two opposite effects of DNA.

Stage III. *Bacteria* **and** *Cyanophyceae.*

1. Isogamy (monoecism)?
2. Homogamy (dioecism)?

Stage IV. *Monadophyta (Flagellatae)*

1. Isogamy (monoecism)	*Protococcales*	*Heterocontae*	*Volvocales*
2. Homogamy (dioecism)	*Desmidiaceae* *Diatomeae*	*Volvocales*	*Chrysophyceae*
3. Anisogamy (dioecism)		*Volvocales*	

Stage V. *Algophyta (Chlorophyta)*

	Cell filament	**Monopodial**	**Dichotomous branching**	**Verticillate**
1. Isozygota (g. monoecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*	*Syphonales*	*Ulotrichales*
2. Homozygota (g. dioecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*	*Syphonales*	*Ulotrichales*
3. Anisozygota (g. dioecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*		
4. Homomorphous (dioecism)	*Siphonocladales*	*Syphonales*	?	*Ulotrichales*

Stage VI. *Bryophyta* **and** *Charophyta*			
1. Isospore (g. monoecism)	*Musci*	*Hepaticae*	*Charales*
2. Homospore (g. dioecism)	*Musci*	*Hepaticae*	*Charales*
3. Anisospore (dioecism)	*Musci*	*Hepaticae*	*Charales*
Stage VII. *Psilophyta*			
1. Isospore (g. and sp. monoecism)	*Hornea* *Rhynia*	*Protopteridium* *Psilotum*	*Calamophyton*
2. Homospore (g. dioecism sp. dioecism)	?	?	?
3. Anisospore (g. dioecism sp. monoecism)	?	?	?
Stage VIII. *Pteridophyta*			
1. Isosporophyllum (g. and sp. monoecism)	*Lycopodinae*	*Filicinae*	*Equisetinae* *Sphenophyllum*
2. Homosporophyllum (g. dioecism, sp. monoecism)	*Lycopodinae*	*Parkeriaceae*	*Equisetinae*
3. Heterosporophyllum (g. dioecism, sp. monoecism)	*Lepidodendron* *Selaginellales*	*Sigillaria* *Hydropterides* *Isoëtes* *Stylites*	*Calamites*
Stage IX. *Pteridospermae*			
1. Isospermy (g. dioecism, sp. monoecism)	*Lepidocarpon*	*Lyginodendron*	*Calamocarpon*
2. Homospermy		?	?
Stage X. *Gymnospermae*			
1. Isospermy (g. dioecism, sp. monoecism)	*Pinaceae* *Taxodiaceae*	?	*Cupressaceae*
2. Homospermy (g. and sp dioecism)	—	*Araucariaceae* *Cordaites(?)* *Ginkgoaceae* *Cycadales* *Podocarpaceae* *Taxales*	*Cupressaceae*
3. Euspermy (hermaphrodite?)	*(Coniferae?)*	*Bennettites*	—
Stage XI. *Chlamydospermae*			
1. Isospermy (monoecism)	—	—	?
2. Homospermy (g. and sp. dioecism)	*Gnetum*	*Welwitschia*	*Ephedra*
Stage XII. *Angiospermae*			
1. Isospermy (g. dioecism sp. monoecism)	*Monochlamydeae*	*Cyperales* *Palmae*	*Verticillatae*
2. Homospermy (g. and sp. dioecism)	*Monochlamydeae*	*Palmae*	—
3. Euspermy (hermaphrodite) (g. and sp. monoecism)	*Dialipetalae*	*Liliflorae*	*(Sympetalae??)*

Natural system of the Landsplants (after the author)

I. Stage **Virophyta**

II. Stage **Anucleophyta**

III. Stage **Monadophyta**

IV. Stage **Algophyta**

(Mykophyta)

1. *Chlorophyta* *(Lichenes)*	2. *Chlorophyta* *(Phaeophyta [?])*	3. *Chlorophyta* *(Rhodophyta(?))*

V. Stage **Bryophyta** et **Charophyta**

1. *Musci*	2. *Hepaticae*	3. *Characeae*

VI. Stage **Psilophyta**

1. *Prolycopsida*	2. *Propteropsida*	3. *Prosphenopsida*

VII. Stage **Pteridophyta**

1. *Lycopsida*	2. *Pteropsida*	3. *Sphaenopsida*

VIII. Stage **Pteridospermae**

1. *Lepidospermae*	2. *Pterispermae*	3. *Calamospermae*

IX. Stage **Gymnospermae**

1. *Isospermae* *(Coniferales)*	2. *Homospermae* *(Cycadales)*	3. *Cupressospermae* *(Cupressales)*

X. Stage **Chlamydospermae**

1. *Gnetales*	2. *Welwitschiales*	3. *Ephedrales*

XI. Stage **Angiospermae**

1. *Dicotyledones*	2. *Monocotyledones*	3. *Verticillatae*

*

This survey is intended as the expression of a concept concerning the polyphyletic evolution of the vegetable kingdom, the probability of which — as demonstrated by the foregoing — is supported by a number of positive facts and natural laws.

The principles of the above concept were laid down by the author as a young botanist 47 years ago in his paper "*Ein Gedanke zur polyphyletischen Entwicklung der Pflanzenwelt*" (Beihefte zum Bot. Centralblatt, 1918.) and expounded in the present paper probably for the last time. Supported by new scientific arguments the discourse might contribute to the elucidation of an extremely important and interesting problem.

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SPOROPHYTA

SPERMATOPHYTA

RAMIF	ALGOPHYTA	BRYOPHYTA	PSILOPHYTA	PTERIDOPHYTA		PTERIDOSPERMAE	GYMNOSPERMAE		CHLAMYDOSP.	ANGIOSPERMAE
		Iso-homosporia	Iso-homosporia	Iso-	homo- heterosporia	Iso-homospermia	Isospermia(Monoecia)	Homospermia (Dioecia)	Homospermia (Dioecia)	Iso-homo- euspermia
	Palaeophyticum						Mesophyticum		Kainophyticum	

MONOP.

MONOPHYTA

Chlorophyceae
Pleurocarpi
Musci
Eriopus
Acrocarpi
Nostra
Rhynia
Psilodendrion
Hornea
Lycopodium
Drepanophycus
Protolepidodendron
Selaginella
Lepidostrobus
Cyclostigma
Lepidodendron
Pinaceae
Lepidocarpon
Geinitzia
Taxodiaceae
Sphenolepidium
Voltzia
Dialipetalae
Degeneria
Gnetum
Monochlamydeae

DICHOT

DOPHYTA

Chlorophyceae
Hepaticae
Asteroxylon
Psilotum
Tmesipteris
Filicinae
Eusporangiatae
Filicinae
Leptosporangiatae
Parkeriaceae
Hydropterides
Isoëtales
Pleuromeia
Sigillaria
Physostoma
Cladoxylon
Hepaticites
Zosterophyllum
Aneurophyton
Megaphyton
Coenopteridales
Asterotheca
Callixylon
Medullosae
Lyginodendron
Odontopteris
Lebachia
Neuropteris
Palaeotaxus
Archeopodocarpus
Williamsonia (Bennettites)
Podocarpaceae
Cycadinae
Taxales
Araucariaceae
Welwitschia
Ginkgo
Cordaites
Baiera
Cayoniales
Cycadeoidea (Bennettites)
Palmae
Liliiflorae
Cyperales
Yuccites
Foerstia
Taeniocrada
Pseudosporochnus
Protopteridium

VERTICILL.

PHYTA

Chlorophyceae
Characeae
Equisetaceae
Protocalamites
Calamophyton
Hyenia
Asterocalamites
Pseudobornia
Sphenophyllum
Schizoneura
Cheirostrobus
Calamostachys
Calamites
Equisetites
Phyllotheca
Neocalamites
Calamitocarpon
(Chamaecyparis)
Cupressaceae
(Callitris)
Ephedraceae
Casuarinaceae

Rajzolta: DÖRFLINGER E.

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A NEW, NINHYDRINE-ISATINE POSITIVE AMINO ACID-LIKE COMPOUND IN THE LEAVES OF RICE PLANT

by

G. PÁLFI

Institute for Plant Physiology of József Attila University, Szeged, Hungary
(Dir.: Prof. Dr. I. SZALAI)

The asparagine concentration of leaves increases parallel to the N amount present in the plants (11, 17). Thous the asparagine test may be the means of detection of N supply of plants. In the course of studying the asparagine test we have pointed out that as a rule the asparagine concentration of rice leaves changes parallel to the total concentration of free amino acids (13). This is also indicated by data of RATNER und UHINA (16). A greater asparagin concentration refers to a better N supply if the total N-content and dry-weight of the same variety is also greater (14). It is very difficult to establish deductions from the amount of free amino acids detected from the plants on their states and the nutrient substrate supply. Amino acid in great amount equally may indicate optimal N supply, vitality, or on the contrary, inadequate P-uptake, decrease of protein synthesis or anything else (1, 2, 3, 18, 20, 22).

It has already been established in pot experiments that the free amino acid content of rice shoots grown in alkalized by N-salts media is considerably higher than that of rice grown with normal nutrient solution — the NPK content of the nutrient medium being the same (14).

It appears that the cause of changes in the amino acid concentration has not been cleared up yet. In the course of our own experiments we aimed to answer the following questions:

1. How does the amino acid concentration in rice leaves change when all the leaves are completely developed?

2. Is there a dependence between total amino acid concentration and total N concentration in leaves of various levels?

3. Does the total amino acid and asparagine concentration change with the degree of N supply?

Materials and Methods

The experiment was carried out in Kopáncs Experimental Plantation. A Dunghan Shali variety was planted 12 March, 1963, and immediately flooded thereafter. The carrying of ammonium sulphate into the soil was done before planting as follows:

1. without fertilization,
2. 434 kg/ha (mediocre amount),
3. 695 kg/ha (high amount).

The area of separated parcels was 50 m². Beginning from flowering (8 August) samples were taken by 8 days, four times all together. Shoots were worked out by leaf-levels. They were fixed at 65° C and dried (air-dry weight). They were ground then fractured with perchloric acid salicil sulphuric acid; total N was measured with a PULFRICH photometer after NESSLER reaction.

Amino acids were detected by ascending paper chromatography. The air-dried plant parts were extracted with 70% ethanol and samples were carried on WHATMAN No 1 paper in four repetitions. The solvent was a butanol-glacial acetic acid-water mixture in a ratio of 2 : 1 : 1. Int two dimensional runs phenol-water of 4 : 1 ratio was applied as the second solvent. The chromatograms were sprayed with ninhydrine and isatin, on applying the methods of "universal standard mixture" and "rapid determination of total amino acid by eluation." In elaborating the new method we have started from KRETOVICS and KASZPAREK (8) and SZALAI's (19) works (13, 14). The essence of the method is that the composition of standard amino acids is similar to the amino acid composition of plant extracts. Therefore single amino acids of the standard run on the same level as the corresponding amino acids of the plant extracts (Figures 1 and 2). On determining the total amino acid content we have sprayed a standard mixture concentration series with ninhydrine on the same paper of the unknown extracts. Eluted spots being fixed by copper salt were examined by photometry. Extinction data of eluted standard spots yield the calibration curve.

Experimental Results

Table I shows measurement data. It appears that the greatest difference was obtained at a leaf length where in some cases the difference exceeds even 70—100 per cent. It also can be seen that increased N supply decreased the extent of tillering, namely the number of shoots by m² is less on these parcels.

Table 1

Rice shoot length and length of leaves, density of shoots during flowering on effect of different amounts of N.

Treatments	Length of leaves, cm				Length of shoots cm	density of shoots m²
	lower 1.	middle 2.	middle 3.	upper 4.		
without manuring (control)	18,2 ±0,93	22,8 ±1,1	23,4 ±1,0	17,2 ±0,81	95,3 ±3,0	246 ±8,7
434 kg/ha $(NH_4)_2SO_4$	25,1 ±1,3	33,1 ±1,0	30,1 ±1,2	18,6 ±0,72	110,7 ±2,6	225 ±10,1
695 kg/ha $(NH_4)_2SO_4$	30,5 ±1,1	41,3 ±1,6	41,5 ±1,8	23,7 ±1,0	105,2 ±3,2	197 ±9,4
695 kg/ha, $(NH_4)_2SO_4$ diseased rice	30,6 ±1,3	45,6 ±1,7	43,2 ±1,9	28,4 ±1,3	105,4 ±3,7	190 ±12,3

On parcels manured with greater quantity of nitrogen the plants were partly lodged during flowering. Leaves became darkish green. The peaks dried-off, brownish spots appeared onthe leaves. Further these plants are called diseased rice.

It had already been published that the maximal number of living leaves of the variety studied is 5 in flowering however, as a rule, it is less, depending on the level of flooding and the nutrition. In the present case the shoots have 3-4 leaves. Figure 1 shows the amino acid content of seedlings with three leaves at three different amino acid concentrations of the universal standard mixture. It appears that the amino acid concentration in rice leaves of various insertions changes considerably upwards. There may be even more than 100 per cent difference between the total amino acid content of the uppermost and lowest leaves (Table IV). Regarding that in flowering 80% of the shoots were of four leaves, further we are referring to their data.

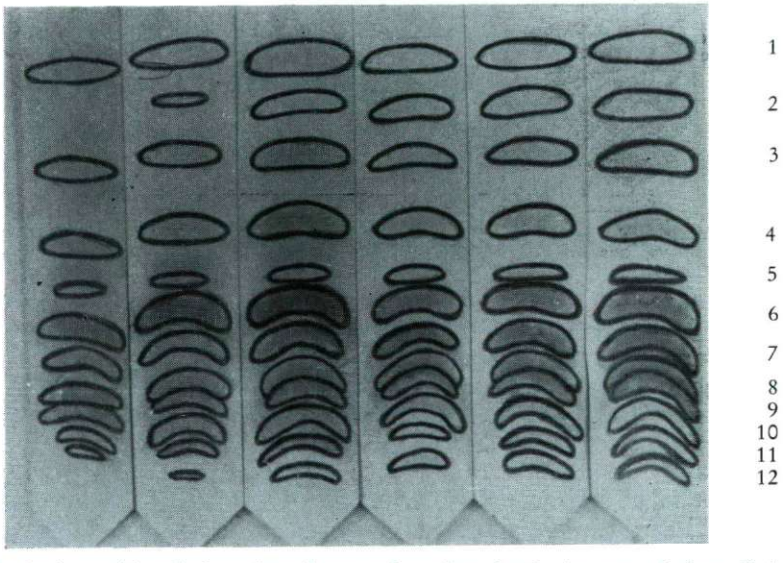

Figure 1. Amino acids of rice plant leaves of various levels in case of three living leaves (control). ABC = lower, middle and upper leaves, DEF = universal standard of plant extract with 25, 37,5 and 50 μg total amino acid content.
Composition of Standard No 3:

1. Leu	1,5 mikrog.	7. Ser., Glu	6,0 mikrog.
2. Phe	3,0 „	8. Gly., Glu-NH_2	3,5 „
3. Val	1,5 „	9. Asp	10,0 „
4 γ-amb	1,5 „	10. Asp-NH_2	8,0 „
5. Pro	5,0 „	11. Lys	1,0 „
6. Ala	5,0 „	12. Cys	4,0 „

The amino acid content in leaves of various levels of 4-leave rice without manuring also increases upwards to the third leaf. That of the fourth, in the uppermost leaf somewhat decreases (Table IV). A similar tendency is observed at rice supplied with 434 kg ammonium sulphate. However, on effect of 695 N

the amino acid content of leaves is compensated. This compensation occurs in case of diseased rice (Figure 2).

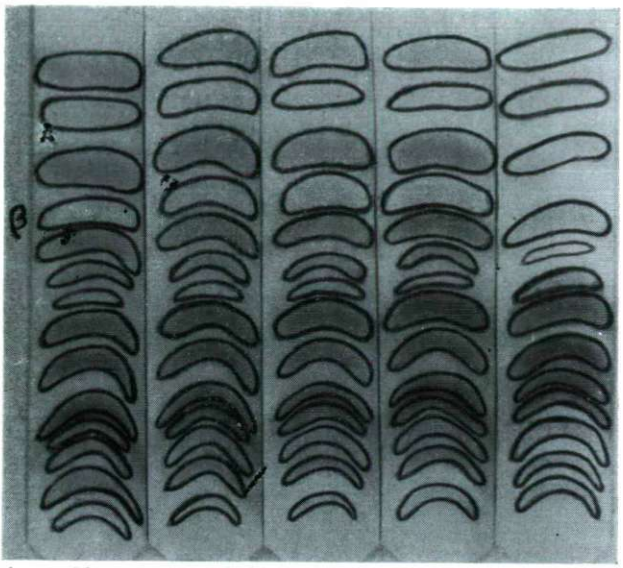

Figure 2. Amino acid content of lodged rice shoots manured with great amount of N by leaves of various levels. ABCD = lower, middle 1, middle 2 and upper leaves. E = Universal standard with 50 μg total amino acid content. Composition: as in Fig. 1. β = unknown amino-acid-like substance.

There is one important quantitative difference between the varieties: an amino-acid-like compound of unknown composition appearing at 0,64 Rf between γ-aminobutyric acid and valine. The spot denoted by us by β is the greatest at diseased rice (Figure 2), it is also considerable at healthy rice treated with 695 kg but here it decreases by levels. It could be observed only to a small extent at seedlings on parcels manured with 434 kg: in the two upper leaves. It could not be detected even in traces at rice without fertilizer (Figure 1). The ninhydrine reaction of the β-substance is not the customary reddish-purple, but bluish. After spraying with copper- or nickel-salt solution it is purple- blue and at spraying with isatin, bluish-green. It does not fluoresce after ultraviolet illumination. It does not give anilinephtalate and antron sugar reaction. In two dimensional chromatograms it is the fastest of all the amino acids of rice, as Figure 4 shows. Figures 3 and 4 also indicate that there is not other difference between diseased and healthy rice as the only β-spot. After a 5 n hydrochloric acid hydrolysis of the vaporized amino acid extract of the diseased rice, carried out for 72 hours at 105 C°, the unknown substance appeared after separation with the same intensity as a blue spot, as without hydrolysis. Thus β-compound is not peptide and is very stable. It does not take part in protein composition: being the free amino acids of the rice leaf homogenisatum removed and the hydrochloric acid hydrolysis of proteins carried out thereafter, it does not appear in the chromatograms. The analysis is further carried on.

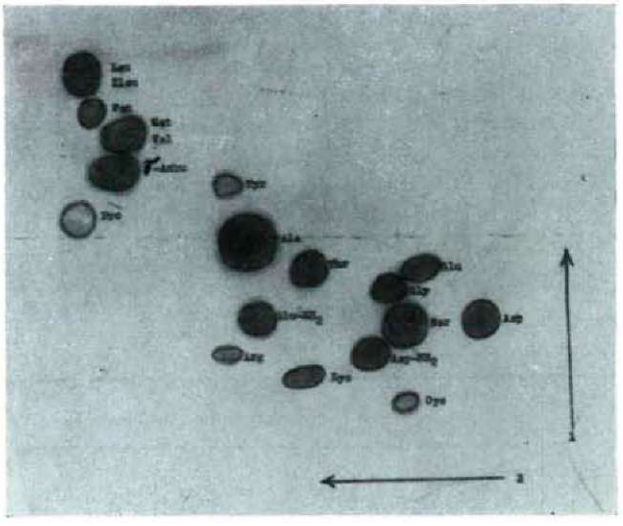

Figure 3. Amino acids of the middle leaves of rice without manuring. 1st direction: butanol-acetic acid-water. 2nd direction: phenol-water. ninhydrine, sprayed with copper salt solution.

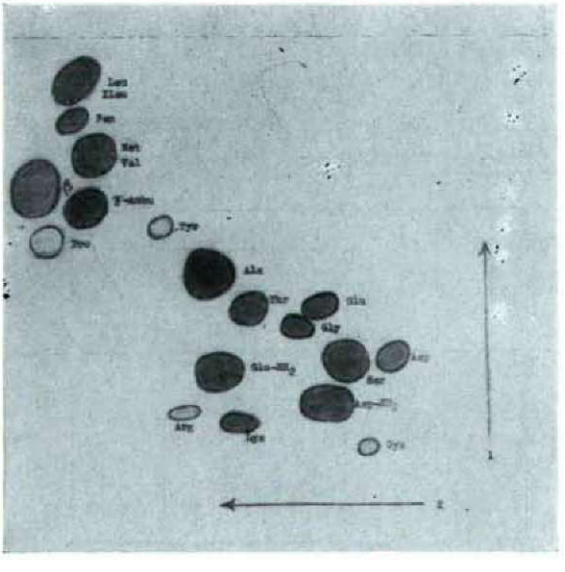

Figure 4. Amino acids of lodged rice shoots manured with great amount of N in their middle leaves. Outer-left spot is the β-substance.

As Table II shows, dry-weight increases parallel to the amount of N corresponding to the leaf-length (Table I) and it is the greatest in case of diseased rice. Total N-concentration increases within the shoots by levels. Being the total N concentrations of the single leaves of various level compared by varieties, it can be seen that there is an increase only at the 695 kg N manuring at the diseased rice. Thus it is very difficult to alter the "critical concentration" of leaves. Taking, however, into consideration the magnitude of dry-weights, too, it seems that varieties manured with N took up considerably more nitrogen from the soil (Table III).

Table 2

Dry-weight of rice leaves by leaves of various levels during flowering

Treatments	Dry, weight, mg.			
	1. lower	2. middle	3. middle	4. upper
without manuring (control)	73 ±2,4	74 ±2,3	80 ±2,7	64 ±2,1
434 kg/ha $(NH_4)_2SO_4$	91 ±3,8	110 ±4,2	100 ±4,3	85 ±3,5
695 kg/ha $(NH_4)_2SO_4$	110 ±4,3	150 ±5,7	150 ±5,5	120 ±4,1
695 kg/ha, $(NH_4)_2SO_4$ diseased rice	160 ±6,1	210 ±7,9	210 ±8,5	160 ±6,4

Table 3

Total N concentration of rice leaves in per cent of dry weight and the total N content in mg during flowering by leaves of various levels

Treatments	1. lower		2. middle		3. middle		4. upper	
	N concentr. %	N content mg	N concentr. %	N content mg	N concentr. %	N content mg	N concentr. %	N content mg
without manuring	0,72 ±0,028	0,53 ±0,017	1,02 ±0,04	0,75 ±0,04	1,10 ±0,05	0,88 ±0,03	1,40 ±0,05	0,89 ±0,03
434 kg/ha $(NH_4)_2SO_4$	0,71 ±0,03	0,64 ±0,028	0,92 ±0,04	1,01 ±0,05	1,10 ±0,05	1,10 ±0,04	1,40 ±0,07	1,19 ±0,05
695 kg/ha $(NH_4)_2SO_4$	0,72 ±0,04	0,79 ±0,03	1,20 ±0,04	1,80 ±0,07	1,40 ±0,06	2,10 ±0,08	1,70 ±0,06	2,04 ±0,09
695 kg/ha, diseased rice	0,92 ±0,042	1,47 ±0,07	1,30 ±0,05	2,73 ±0,09	1,50 ±0,07	3,15 ±0,14	1,40 ±0,06	2,24 ±0,09

Data of total amino acid content (Table IV) also indicate the increase of concentration by level of shoots manured with mediocre amount of nitrogen and of the control. But the concentration is compensated here too in case of great N amount. Asparagin concentration of the leaves generally also increases by levels and it reflects very well the degree of N supply.

Table 4

Total amino acid and asparagin concentration of rice leaves in per cent of dry weight by leaves of various levels during flowering

Treatments	1. lower		2. middle		3. middle		4. upper	
	total amino acids	aspara gine	total amino acids	aspara gine	total amino acids	aspara gine	total amino acids	aspara gine
without manuring	0,52 ±0,04	—	0,88 ±0,08	0,022 ±0,002	1,25 ±0,09	0,035 ±0,003	1,12 ±0,10	0,027 ±0,003
434 kg/ha $(NH_4)_2SO_4$	0,86 ±0,07	0,033 ±0,003	1,12 ±0,09	0,062 ±0,006	1,34 ±0,11	0,076 ±0,007	1,27 ±0,09	0,074 ±0,007
695 kg/ha $(NH_4)_2SO_4$	1,16 ±0,10	0,075 ±0,007	1,35 ±0,11	0,093 ±0,008	1,30 ±0,10	0,097 ±0,008	1,31 ±0,11	0,103 ±0,010
695 kg/ha, diseased rice	1,27 ±0,11	0,106 ±0,010	1,21 ±0,10	0,124 ±0,011	1,14 ±0,09	0,121 ±0,011	1,47 ±0,12	0,124 ±0,010

From all these data it is clear that the constant results of analyses were obtained with the middle leaves of rice seedlings, and in the following we give data of the second leaf from teh top.

Dry weight amounts obtained from flowering till ripening increases parallel to the amount of N supply (Figure 5). The total concentration of leaves does not give such a clear picture, although it somewhat increases proportional to the degree of N nutrition. It can be seen that the total N concentration of the leaves, independently of the treatment, markedly decreases during ripening. To a certain degree the extent of N supply can be seen from the total amino acid concentration of the leaves, too (Figure 6); it has a decreasing tendency during ripening but it has a sudden raise at the last, September sample. This fact may be ascribed to the emptying of the leaves before ripening, and the rushed translocation of the substances, respectively. The asparagine concentration of the leaves well shows the amount of N-supply (Figure 6).

The yield is significant because of the uneven diseased spots. Calculated for hectares it is 4,13 ton for the control; 4,56 ton for the variety manured with 434 kg; 3,28 ton for that manured with 695 kg. (Data and yield are given by. P. ADAMIK for which I express my thanks here, too.)

For the yield control a precisely evaluated analysis was carried out (Table V). It appeared that the panicle grain number, disregarding treatment, as a rule is low. It somewhat increases as well as the panicle length, when the N amount is increased. The thousand grain weight slightly decreases for the mediocre N amount, and with 25,8% for the great N amount as compared

Table 5

Yield analysis: panicle length and panicle grain number of rice: total N concentration of grain yield and thousand grain weight

Examination	without manuring	434 kg/ha $(NH_4)_2SO_4$	695 kg/ha $(NH_4)_2SO_4$
Length of panicle cm.	13,6 ±0,21	13,8 ±0,18	14,6 ±0,25
Grain number/panicle	42 ±1,8	47 ±2,1	54 ±2,6
Weight of 1000 grain	30,2 ±0,42	29,5 ±0,53	22,4 ±0,61
Total N concentr. of grain yield, %	0,56 ±0,022	0,60 ±0,019	0,65 ±0,025

with the control. Total N content of the grain yield did not give considerable difference. Data of yield analysis together with the density of shoots beyond any doubt testify the yield decreasing effect of the unisided N fertilization.

Figure 5

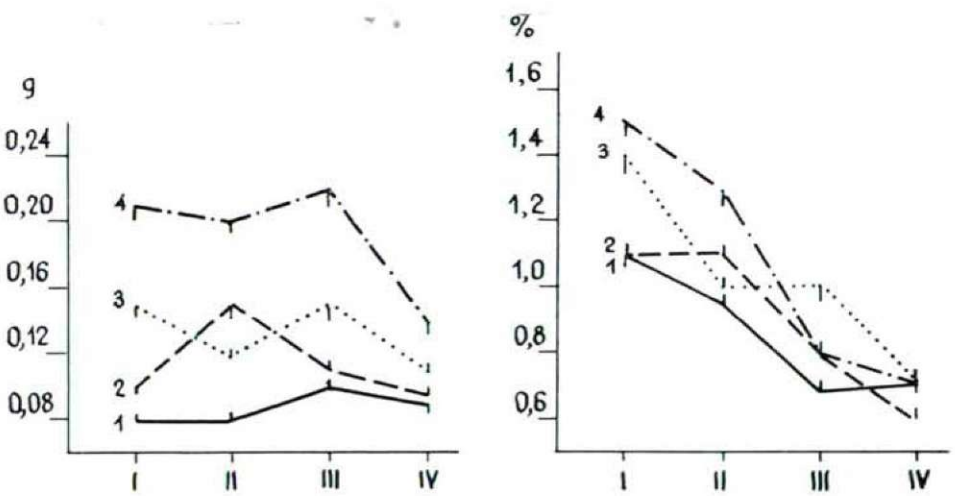

Figure 5. Dry-weight of middle leaves (on the left) and total N concentration as per cent of dry weight (on the right). I = flowering, II—IV = ripening. 1 — without manuring (controll); 2 — 434 kg/Ha N salt; 3— 695 kg/ha N salt, lodged rice. Length of liens means the magnitude of mean error.

Figure 6

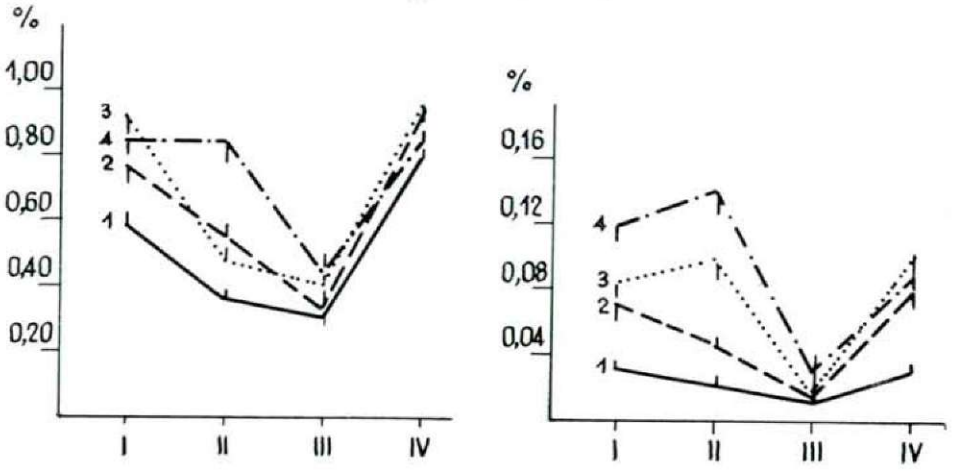

Figure 6. Total amino acid concentration of middle rice leaves (on the left) and asparagine concentration as per cent of dry weight (on the right). I = flowering, II—IV = ripening. 1—4 N salt magnitude as in Figure 5.

Discussion

Symptoms observed at N supply of great amount (Table I) agree with the P-deficiency symptoms described by HUGUET (7), but the relative P-deficiency of rice has already been described by us, too, (15) as well as by GRIST (5).

Increased amount of N did not cause considerable change in N concentration of the leaves (Table III), but the total N content of the leaves was markedly increased.

The amino acid content of the shoots by levels increases suddenly from bottom upwards in case of small N nutrition (Table IV). This fact can be ascribed to the ageing of the leaves, as pointed out by MOTHES (10) and PARTHIER (12). Then the decomposition of proteins and a rapid dislocation of amino acids occurs in the aged leaves. On effect of 695 kg N manure the difference between the amino acid concentration of the leaves of various levels disappears (Figure 2). Thus in case of increased N nutrition the leaves of various levels were saturated with free amino acids. This saturation may indicate the degree of N supply. This tendency can be observed at the asparagine concentration of the leaves of various levels, too, but to a less extent only. Thus the asparagine concentration of the single varieties by leaves of various levels increases according to the amount of N nutrition. (Table IV).

From our data it appears that a quantitative change of the amino acids is first of all caused by the N-manuring. Qualitatively a considerable difference is the positive ninhydrine and isatin spot at 0,64 Rf, which in the second dimension runs up to the highest Rf. This spot denoted by β may be one of the amino increases parallel to the magnitude of N supply, after a thoroughful study it can be an indicator of the magnitude of N nutrition.

In yield analysis the low thousand grain weight is a result of the bad fertilization as it had already been referred to by VÁMOS (21) and HARANJAN (6) in connection with N overnutrition.

Summary

In the course of study of free amino acids three characteristic features of the effect of great amount of N have been observed:

1. The amino acid concentration of leaves of various levels without fertilization and supplied with 434 kg ammonium sulphate per hectare rushedly increases upwards. At rice manured with 695 kg per hectare the concentration of the leaves is almost the same, especially at diseased rice. Thus on effect of great amount of N the leaves of various levels are saturated with free amino acids.

2. The asparagin concentration of the leaves increased parallel to the degree of N nutrition, especially on effect of increased amount of N.

3. New ninhydrine and isatin positive amino acid-like compound was pointed out at 0,64 Rf, between γ-aminobutyric acid and valin, which does not constitute protein. The amount of this substance denoted by β increased parallel acid derivates or precursors detected by MARÓTI (9) and FOWDEN (4). Since the amount of substance of unknown com position pointed out in the β-spot to the degree of N nutrition. Most of it was found in the diseased rice, in the control it could not be detected.

On effect of unisided N manuring the rice shoots show symptoms of P deficiency. The magnitude of N nutrition hardly could be detected in the N concentration of the leaves, but very well in dry weight and total N content.

The yield-decreasing effect of great amount of N reveals itself in the slight tillering and bad fertilization.

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GERMINATION- AND GROWTH-INHIBITING SUBSTANCES IN RICE GRAINS

I. Studies on the effect and properties of the inhibitors in the covering structures

by

M. VARGA

Institute for Plant Physiology, University of Szeged, Hungary
(Dir.: Prof. Dr. I. SZALAI)

Introduction

Experiments aiming at the physiological and biochemical examinations of the growth of rice varieties (VARGA 1963, 1964) drew the attention to the germination- and growth-inhibiting substances in the rice grains.

The presence and physiological role of the germination- and growth-inhibitors in the different dry seeds and fruits is well known from the literature. Numerous papers deal also with the examination of the effect and physiological significance of the inhibitors localized in the caryopsis — mainly in the layers covering the grains — of cereals such as wheat (MOSHEOV 1938, MIYAMOTO and EVENSON 1958, MIYAMOTO et al. 1961), oat (ELLIOT and LEOPOLD 1953, TUNG-FANG 1957, KÖVES 1957, PEERS 1958, FRITZGERALD 1959), wild oat (KOMMEDHAL et al. 1958, BLACK 1959), barley (POLLOCK 1959) and rye (FURSTE 1958). Some authors attempted to discover the chemical nature of the inhibitory substances too (MIYAMOTO and EVERSON 1958, MIYAMOTO et al. 1961, KÖVES 1957, VARGA and KÖVES 1961).

On the other hand, relatively few data are available concerning the germination- and growth-inhibiting substances in the rice caryopsis. ULALI et al. (1960), further NAIR and SHADEVAN (1962) on experimental basis concluded that rice covering structures contain inhibitory substances. MIKKELSEN and SINAH (1961) extracted substances, inhibiting the germination and the growth, from the rice grains. KÖVES and ÁCS (1963) studying the properties of rice grains of reduced germinating power demonstrated certain inhibitors in the husk and grain. ROBERTS (1961), however, found — neither in the rice husk nor in the grains — any germination- and growth-inhibiting substances extractible with water or ether which is at variance to other data. But authors demonstrating inhibitors from the rice grains carried out no detailed examinations concerning the effect and charachteristics of these substances.

In the first part of our paper we wish to elucidate the rate of the effect of the effect of the inhibitors in covering structures on the germination and growth as well as the principal properties of the inhibiting substances.

Material and method

As it is known from literary data and earlier examinations that the inhibiting substances of the rice grains are localized in the *pericarpium* and *testa*, further in the husk (*lemma* and *palea*); bran, resulting from dehusking and available in large quantities, was used for experiment. The bran — dehusked from *Dunghan Shali* harvested in 1962 — was obtained from the Dehusking Mill and Marketing Cooperative of Karcag. The bran contains the tissues of the husk, *pericarpium* and *testa*, moreover the *aleuron* layer of the endosperm — though in a smaller quantity compared with that of the former. The bran was stored in dry condition at 0°C.

Extraction of the inhibitors. 50 g of rice-bran with water (100 ml) was shaken at room temperature for 6 hours and the suspension was centrifuged. The supernatant fluid was completed with water to 100 ml and the obtained extract was considered as a stock solution. Then a serial dilution was prepared ranging from 2·5× to 100× and their germination- and growth-inhibitory effect and properties were examined with rice-embryo and lettuce seed germination test, further with rice and oat coleoptile section test as well as with lettuce hypocotyl test.

Rice-embryo test. The embryos were cut from *Dunghan Shali* grains of 96% germinating power, harvested in 1962. 20 excised embryos were placed with the endosperm side down in a Petri dish of 6 cm ∅ on a disc of double filter paper wetted with 3 ml of test solution. The dishes were then incubated at 25°C partly in dark, partly in light.

Lettuce seed test. 50 seeds (*Lactuca sativa* **L.** „Böttner") were germinated in an 8 cm ∅ Petri dish at 25°C in light, on double filter paper discs wetted with 4 ml test solution. Occasionally, beside the lettuce seeds — in the same way — intact or dehusked rice grains, mustard, millet, panicum and poppy seeds were also used for germination test. In every case the germination per cent, the germinating power as well as the length of the shoot and root of the seedlings were observed against the time and concentration.

Rice and oat coleoptile section test was made as described in our earlier papers (VARGA and FERENCZY 1957).

Lettuce hypocotyl test was carried out with FRANKLAND—WAREING's technique (1960) modified by WHEELER (1962).

Results and discussion

The cause of the effect of husk delaying germination

According to ROBERTS (1961) the husk of the rice grains contains no inhibitors; its germination delaying effect is solely due to its preventing the gas-exchange between the grain and environment. On the other hand, the above mentioned authors assumed i. e. found inhibitors in the husk.

Consequently first, as an informative experiment, we compared the germination of intact and dehusked grains and the growth of the seedlings. The germination of dehusked grains in the presence of the removed husks was also examined. In every case 50 rice grains were put in a 10 cm ∅ Petri

dish on a double filter paper wetted with 5 ml water. Some of the dishes in dark, others in light were incubated at 25°C. Results are shown in Fig. 1 and 2. According to Fig. 1 the germination has been prevented by the husk not only mechanically but also by its watersoluble inhibitors, surely the husks removed from the grains and put in the Petri dishes exerted also a certain inhibitory effect. From our data it seems that the prevention of water- and gas-exchange by the husk and the inhibitor content of the husk play roughly equal part in delaying the germination. It is to be noted that no difference was between the germination of the grains incubated in dark and light.

The presence of the husk has also an effect on the initiate growth of the rice seedlings (Fig. 2): the coleoptile- and rootlength of the seedlings in the three samples shows the same differences as seen in the germination.

Therefore the husk of the rice grains — like other cereals — contains germination- and growth-inhibitory substances.

Examination of the effect of water extract

The rate of germination inhibitory effect of the dilutions (2,5×, 5×, 7,5×, 10×, 20×, 40×, 60× and 100× dilutions) prepared from the stock solution (0× dilution) considerably inhibit the germination. The higher dilutions influence somewhat less the germination per cent, but they retard the germination. The dilutions 60×, 80× and 100× proved to be ineffective. The results of the series incubated in dark and light were practically identical

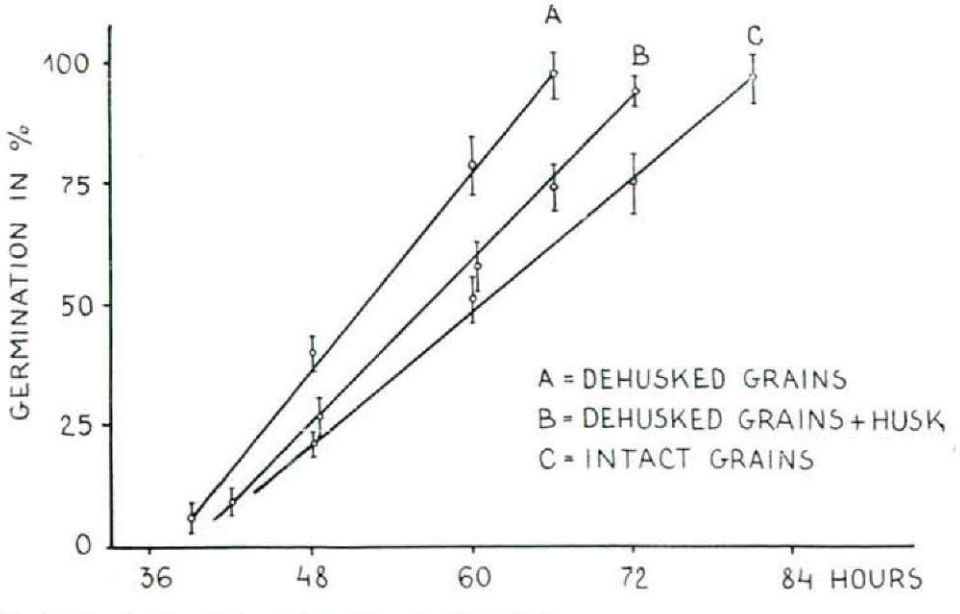

Fig. 1. Germination of rice grains with and without husk.

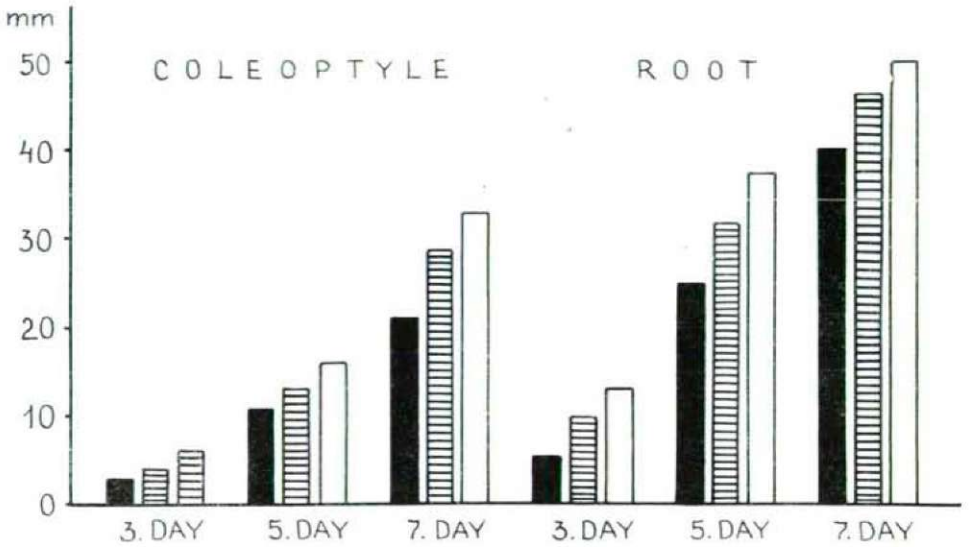

Fig. 2. Growth of rice seedlings obtained from intact and dehusked grains. (Black columns= intact grains, lined columns = dehusked grains + husk, white columns = dehusked grains).

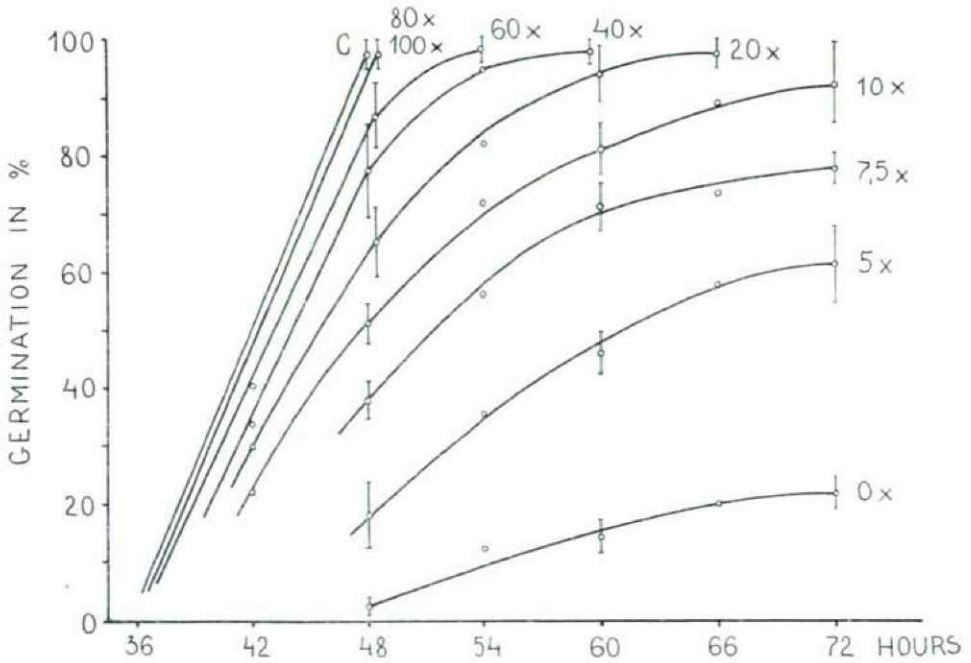

Fig. 3. Germination of rice embryos in different dilutions of bran extract. (C = control.)

The water extract inhibited the germination of the mustard, millet, panicum, poppy and lettuce seeds too, and considerably more than that of the rice embryos. Of the seeds used, the extract exerted the strongest effect on the lettuce, consequently later we employed lettuce seeds beside rice embryos to measure the inhibitory effect. Fig. 4 presents the effect of the serial dilutions

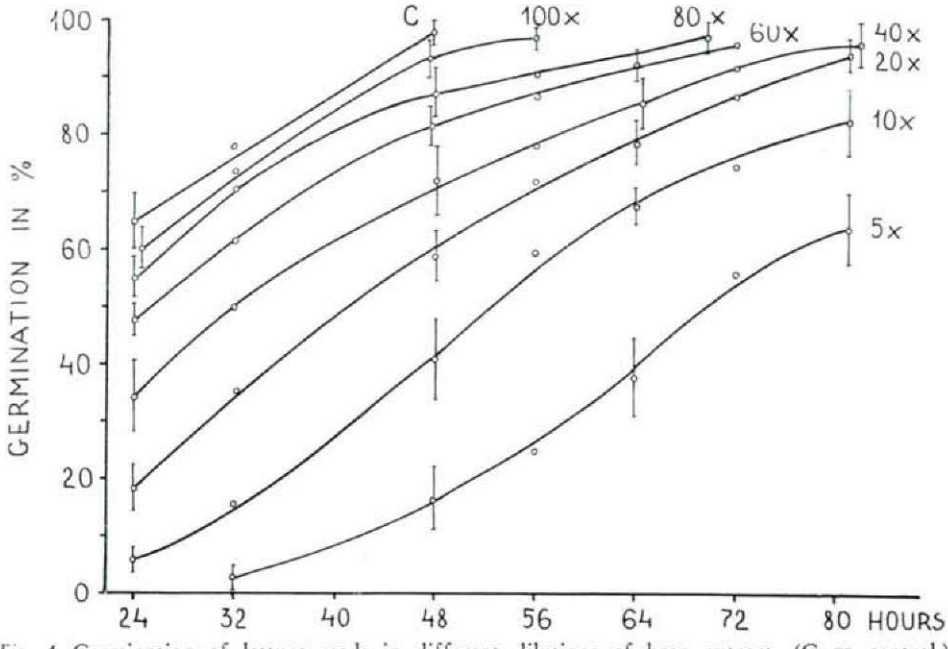

Fig. 4. Germination of lettuce seeds in different dilutions of bran extract. (C = control.)

of the bran-extract on the germination of lettuce seeds. In the stock solution and in 2,5× dilution the seeds did not germinate at all, the further dilutions — in proportion to the concentration — significantly diminished and delayed, respectively, the germination.

The inhibitory substances occurring in the covering structures of rice grain delay least of all the germination of the rice, and to the highest degree that of the lettuce seeds, of the seeds used as test in our experiments.

The water extract and its dilutions have reduced also the growth of the seedlings. Fig. 5 and 6 show the length of the root and shoot of the seedlings — rice and lettuce in water extracts — in the 72. hour. In the figures is shown also the rate of growth in percent of the length of the control. According to the results the inhibiting effect, in rice (Fig. 5) is more pronounced in the growth of the seedlings than in the germination; i. e. the length of the roots and coleoptiles is more sensitive test than the germination itself. It is worth mentioning that MIYAMOTO et al. (1961) experienced the same related to wheat.

It is remarkable that in the case of rice (Fig. 5) the root, while in the case of lettuce the hypocotyl is more sensensitive to the inhibitory effect; the different species, therefore, variously behave in this respect.

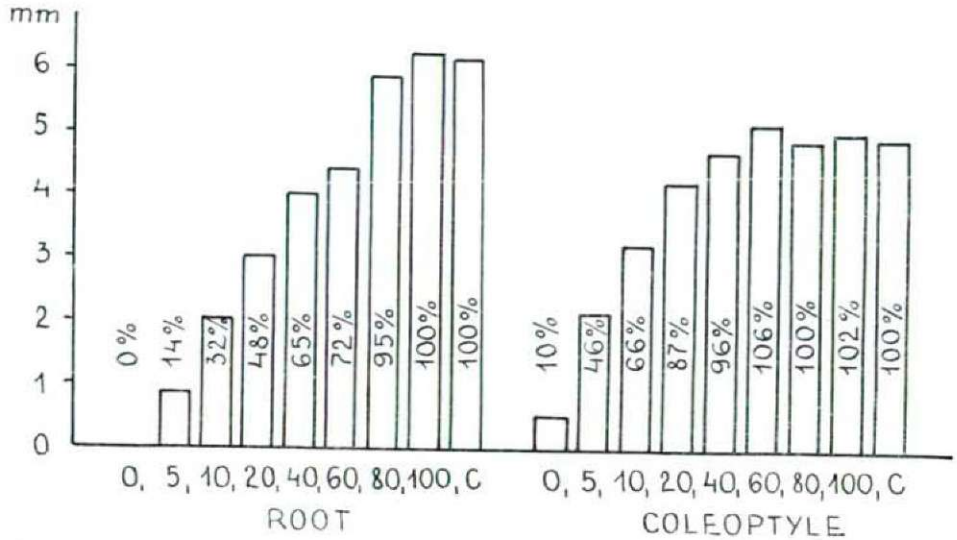

Fig. 5. Growth of the root and shoot of rice seedlings in the different dilutions of water extract, in the 72. hour.

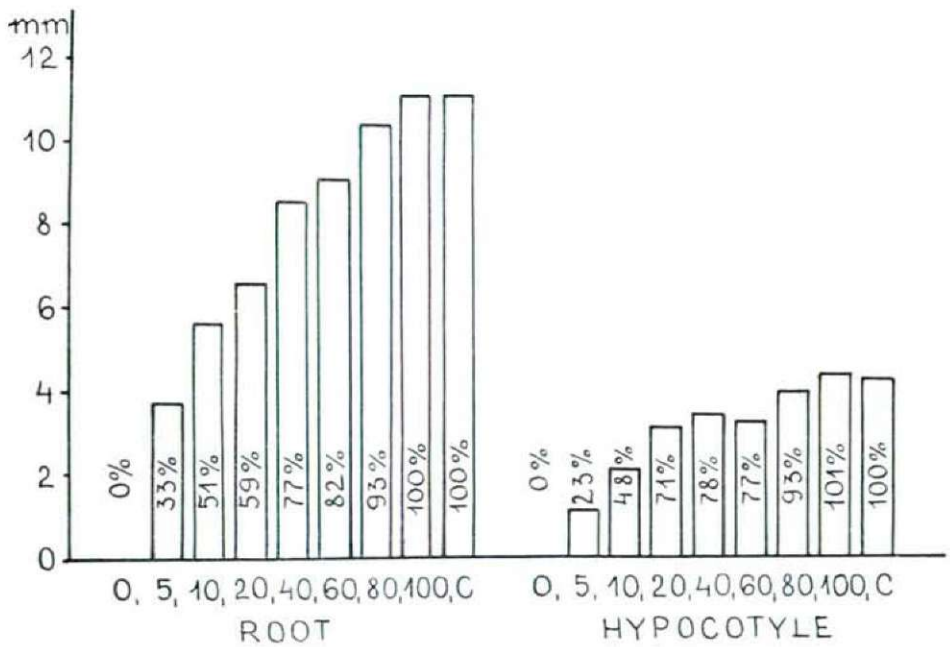

Fig. 6. Growth of the root and shoot of lettuce seedlings in the different dilutions of water extract, in the 72. hour.

Behaviour of the inhibitors to heat

The different dilutions of the water extract were kept at —15, +2, 20, 60 and 100°C for 24 and 48 hours following extraction, thereafter the inhibitory effect was examined with rice embryo and lettuce seed test. The results are summarized in Table I. and II. Accordingly, the activity of the extracts kept at —15°C did not change whereas the activity at +2, 20 and 60°C decreased in the ratio of the rise in the temperature, on the other hand at 100°C it increased. The average activity-change observed in the two tests following heat treatment was:

It follows that a part (the greater part) of the substances occurring in the covering structures of rice grains are thermostabile, the other part (the smaller one) is thermolabile. The rise of the inhibitory effect of the extracts kept at 100°C for 24 or 48 hours is likely to be attributed to the fact that other,

Temperature	Rice embryo	Lettuce seed	
— 15°C	0 %	0 %	Unchanged activity
+ 2°C	1,6%	2,3%	Change within the limit of error
+ 20°C	10,3%	11,0%	Decreased activity
+ 60°C	15,1%	17,3%	Decreased activity
+100°C	8,1%	6,2%	Rise of activity

Hours	Dilution 5×					Dilution 10×					Dilution 20×				
	—15°	+2°	+20°	+60°	+100°	—15°	+2°	+20°	+60°	+100°	—15°	+2°	+20°	+60°	+100°
36	—	—	—	—	—	—	—	—	8	—	—	3	10	15	—
42	—	—	4	11	—	20	25	29	35	10	30	35	40	46	15
48	19	24	33	50	—	40	40	47	60	21	48	52	60	65	35
54	33	40	51	62	20	56	63	66	72	40	69	74	80	80	50
60	45	43	60	71	40	78	68	85	85	52	80	80	83	85	73
66	60	70	80	80	56	84	86	90	90	78	90	90	91	90	80
72	63	72	80	90	65	87	92	95	96	85	95	97	96	96	90

Table I. Germination per cent of rice embryos in rice bran extracts previously treated at different temperatures. (Control is 97% in the 48. hour.)

Hours	Dilution 5×					Dilution 10×					Dilution 20×				
	—15°	+2°	+20°	+60°	+100°	—15°	+2°	+20°	+60°	+100°	—15°	+2°	+20°	+60°	+100°
24	—	—	—	3	—	8	11	14	25	18	18	23	58	50	15
32	—	7	5	9	8	23	37	35	51	23	38	49	72	68	33
40	8	14	13	20	11	49	56	57	68	42	55	67	79	82	47
48	15	24	24	32	16	54	67	72	77	54	62	72	80	85	60
56	31	35	41	49	24	64	75	79	84	59	77	85	90	94	75
64	48	51	61	66	37	72	81	84	89	66	82	90	92	95	83
72	62	64	73	76	51	77	86	88	94	75	90	93	95	96	89
80	72	78	82	87	65	80	89	89	95	81	93	96	94	97	95

Table II. Germination per cent of lettuce seeds in rice bran extracts previously treated at different temperatures. (Control is 96% in the 48. hour.)

more active inhibitory substances are produced due to the formation of certain decomposition products, i. e. to the reaction of some components. It is also possible that at 100°C the decomposition of some substances being able to counteract the inhibitory effect lead to the rise of the activity.

Stability of the inhibitors in vitro

Examining the stability of the inhibitory substances of water extract, its dilutions were kept at +2°C for 6 weeks measuring their activity weekly. (The extracts can not be kept at room temperature for a longer period without infection, administration of antibiotics influences also the germination of the test-seeds and autoclaving, according to the earlier experimental results, is not possible without activity-change). At +2°C, in aqueous solution, in 6 weeks, $5{,}5 \pm 4{,}2\%$ of the activity was lost which being about equal with the standard error can not be taken into account.

The quantity of the inhibitory substances extractable with water from the dry bran practically did not change for 8 weeks following dehusking, measuring weekly.

Interaction between the inhibitors and indoleacetic acid

As the results show that the inhibitory substances of the rice-bran retard the growth of the seedlings to a greater extent than the germination, we examined the interrelationships in the action of these substances and of IAA. The effect of the different concentrations of the bran-extract on the elongation — in the presence of 10^{-3}—10^{-6} M IAA — was measured with rice and oat coleoptile section test. Fig. 7 shows the results obtained with rice coleoptile

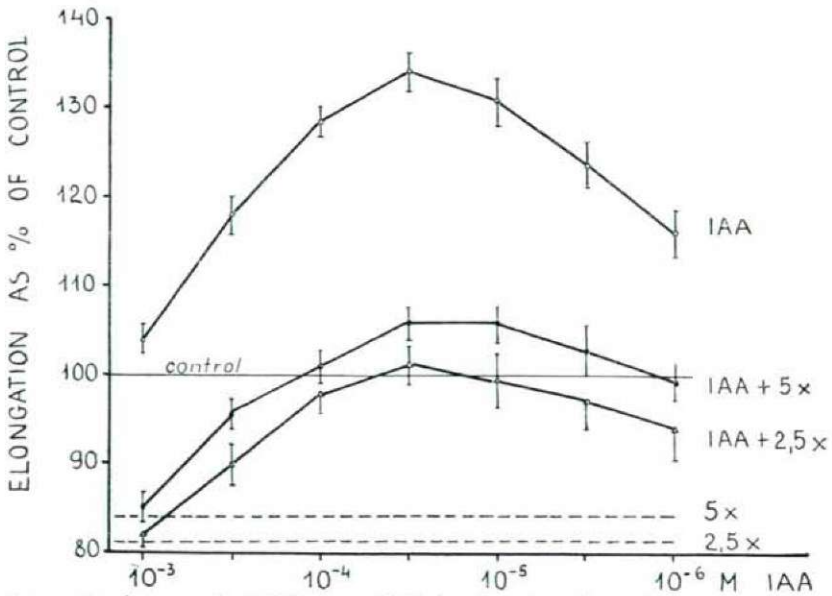

Fig. 7. Interaction between the inhibitors and IAA in rice coleoptile section test. ($s = \pm 4{,}2$; $s_x = \pm 0{,}59$; $s\,\% = 5{,}5$; $n = 50$).

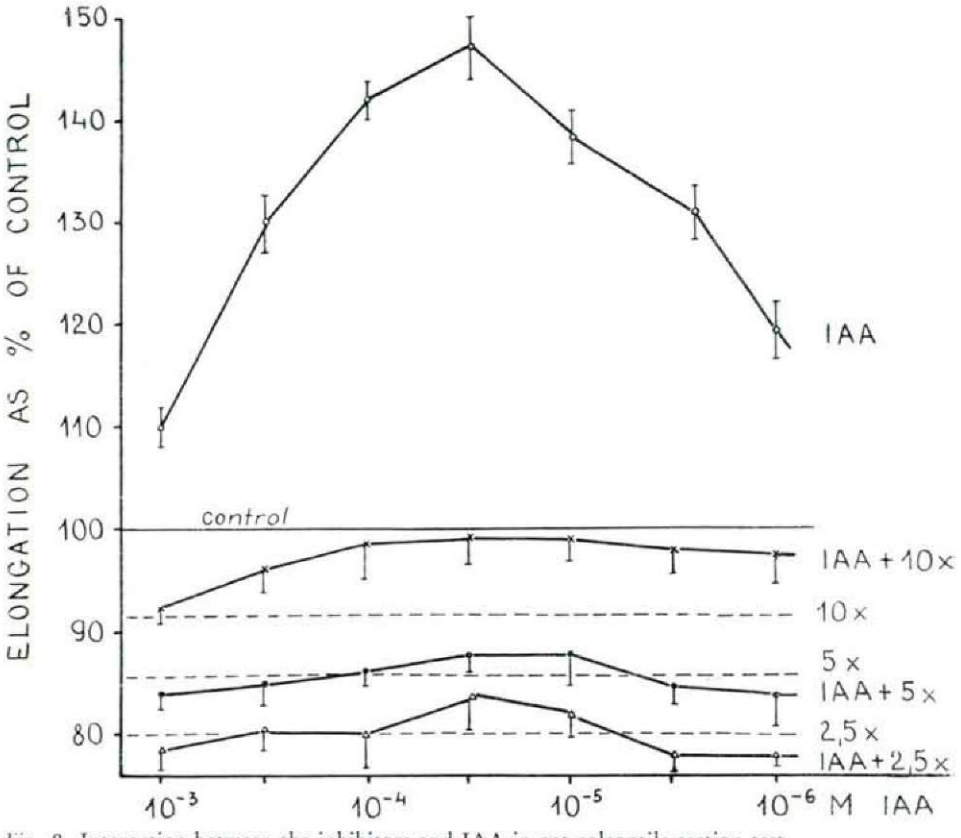

Fig. 8. Interaction between the inhibitors and IAA in oat coleoptile section test. ($s = \pm 4{,}2$; $s = \pm 0{,}63$; $s\,\% = 5{,}02$; $n = 50$).

sections. On the figure the degree of the elongation of rice coleoptile sections can be compared in pure IAA solutions, in the dilutions (2,5× and 5×) of the bran-extract, moreover in simultaneous application of inhibitors and of IAA. The dilution 2,5× and 5× considerably diminishes the effect of IAA; whereas the auxin counterbalances to a certain extent the growth-inhibitory activity of the extracts. On the basis of these results the reduced growth of the shoot of rice seedlings treated with bran-extract, can be explained.

In a still higher degree the auxin-counterbalancing effect of the extracts is shown in the oat coleoptile section test (Fig. 8). Here the dilutions 2,5×, 5× and 10× diminish the effect of the IAA concentrations to such an extent that the elongation of the sections remains below that of the control in every case; and the effect of the auxin can be observed only in the case of dilution 10× to the extent over the limit of standard error. Consequently the oat test is more sensitive to the inhibitory substances of the rice-bran than the rice itself. It may be mentioned that according to GRACZA's results (1957) the rice coleoptiles have the smallest auxin-sensitivity among the cereals.

Interaction between the inhibitors and gibberellins

It is known that the GA generally stimulates the seed germination and the elongation of the stem cells, i. e. the longitudinal growth of the shoots. Now the question arises whether the inhibitors in rice bran extract are able to reverse also this effect of GA.

Therefore we studied the rate of the germination of the rice embryos in the presence of these inhibitors and of the GA together, in different concentrations (Fig. 9). According to the results the water extract, in 2.5×, 5× and 10× dilutions, significantly retards the germination stimulatory effect of the GA; whereas the GA — in the proportion of the concentration — reduces the germination inhibitory effect of the inhibitors. On the basis of our data the inhibting effect due to 10× dilution is reversed only by 100 ppm GA.

Interaction of similar character was noted also in the germination of lettuce seeds (Fig. 10), with the difference that, the lettuce seed being more sensitive test, here the germination retarding effect of the inhibitors is still more strongly shown against the GA. In this case the inhibition due to dilution 20× is ceased by the presence of 100 ppm GA.

The inhibitors of the rice bran prevent also the elongation stimulatory effectiveness of the GA on stem cells. It is seen in Fig. 11 how much is reduced the GA-induced elongation of the rice coleoptiles by the 2,5×, 5× and 10× dilutions of the extract; and this inhibitory effect can be completely reversed only by a relatively larger quantity of the GA. In an earlier work (1964) we demonstrated that the native GA content in rice seedlings is insignificant related to the GA quantity added from outside.

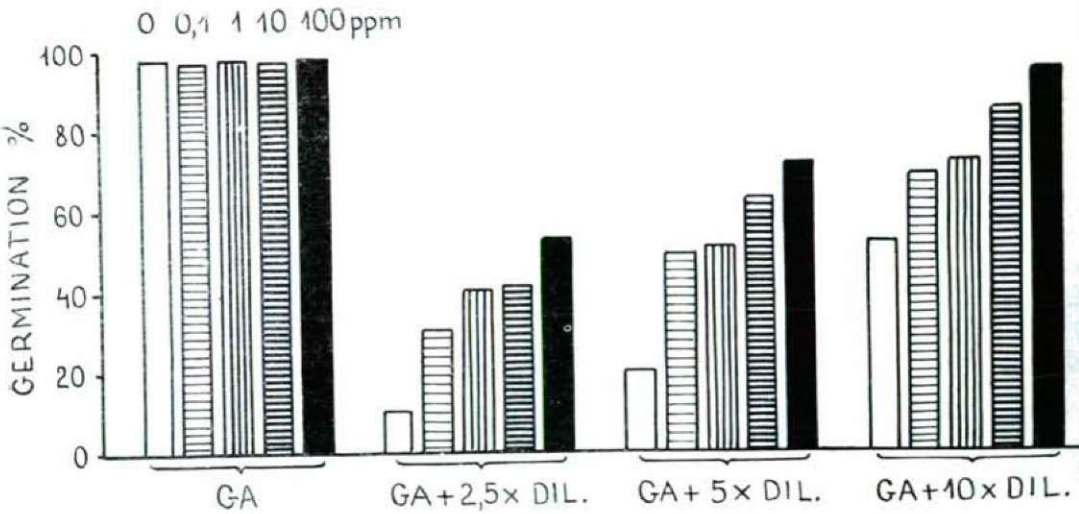

Fig. 9. Germination of rice embryos in simultaneous application of different dilutions of the inhibitors and of GA, in the 48. hour.

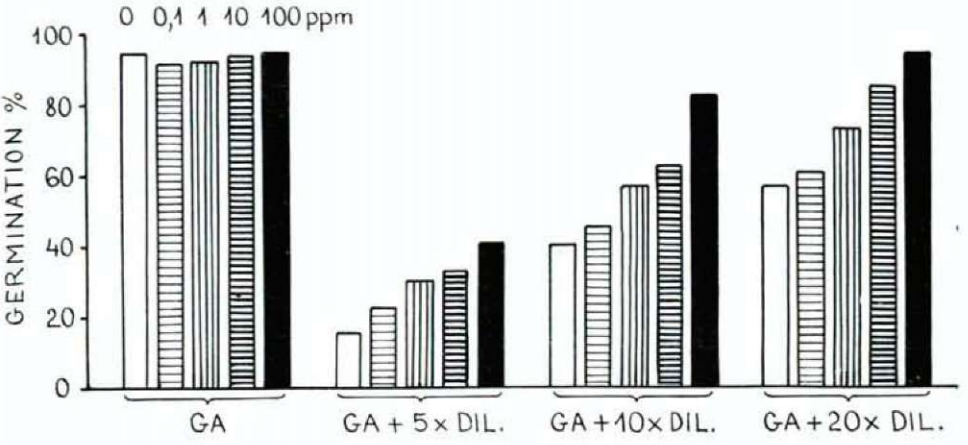

Fig. 10. Germination of lettuce seeds in simultaneous application of different dilutions of inhibitors and of GA, in the 120. hour.

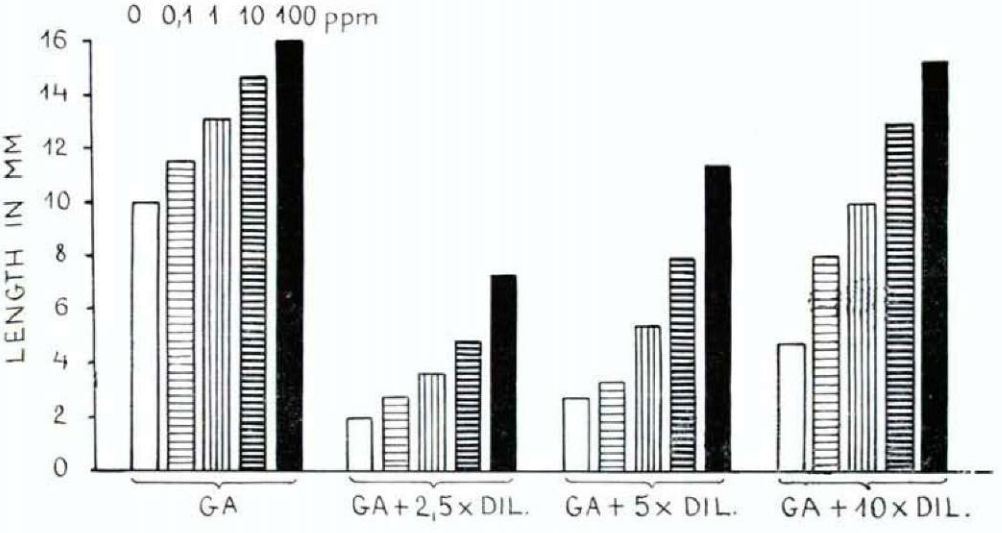

Fig. 11. Growth of the shoot of rice seedlings in the presence of different dilutions of the inhibitors and of GA, in the 120. hour.

The inhibitory substances are able to detain the growth stimulatory effect of the GA, in the highest degree, in the lettuce hypocotyl test (Fig. 12). This is one of the most sensitive tests, so it is very frequently used to demonstrate the gibberellins (FRANKLAND and WAREING 1960, WHEELER 1962, VARGA 1964). The growth reaction of the lettuce hypocotyls to GA — as shown in Fig. 12 — is, to a considerable extent, reduced by the inhibitors of the rice bran and no doubt by other natural inhibitory substances too.

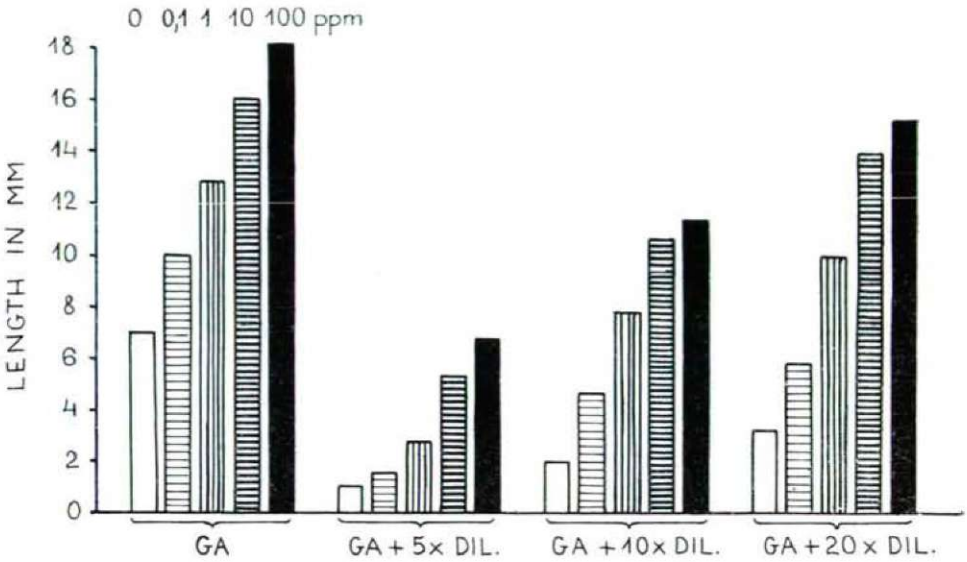

Fig. 12. Interrelationships in the effect of rice bran inhibitors and of GA, in lettuce hypocotyl test. ($s = \pm 1{,}84$; $s_{\bar{x}} = \pm 0{,}33$; $s\,\% = 16{,}3$; $n = 75$.)

Our data are confirmed by CORCORAN et al. (1961) who demonstrated that the extract of some seeds and fruits (e. g. *Ceratonia siliqua*) is able to detain the elongation induced by GA. These facts indicate that the GA content of natural plant extracts can be really determined with biological tests only by a careful separation of the gibberellins from other substances.

Solubility of the inhibitors in organic solvents

50 g of rice bran previously soaked in water was extracted with 100 ml of natural plant extracts can be really determined with biological tests only by were evaporated and the residue was solved in water. The inhibitory effect of the obtained solutions was examined with lettuce seed and lettuce hypocotyl test. In every case smaller or larger germination- and growth-inhibition was observed suggesting that the inhibitory substances, or at least some, are solubile in these organic solvents.

The separation of fractions of different solubility from the water extract and the detailed examination of the effect of single fractions and of their properties is being treated in a subsequent paper.

Summary

Examining the germination- and growth-inhibitory effect and properties of the water extract of the covering structures of rice grains the following results were obtained:

1. The rice husk — alike other cereals — contain germination- and growth-inhibitory substances. The inhibitor content of the paleae play a significant part in retarding the seed germination by the husk.

2. The water extract of the bran and its dilutions, depending on the concentration, inhibit the germiation of the rice embryos and other seeds. Of the seeds used as test object the inhibitory substances inhibit the least the germination of rice and in the highest degree that of lettuce seeds.

3. Inhibitors in the bran of rice reduce the growth of the root and shoot of rice and lettuce seedlings too. In the case of rice the root is more sensitive to the inhibitory effect while in the case of lettuce the hypocotyl.

4. The greater part of the inhibitory substances is thermostabile and the smaller one is thermolabile. At 100°C in the extract, due to certain decompositions or certain reactions of the components, other inhibitors, more active than the original ones, are formed.

5. The inhibitors are stabile at room temperature and at +2°C; some of them are solubile also in methanol, ethanol, chloroform and ethylether.

6. The inhibitors are able, to a considerable extent, to retard the effect of IAA and of GA on the cell elongation and on the stimulation of the germination respectively; whereas IAA and GA, in a certain degree, reduce the germination- and growth-inhibitory activity of these substances.

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ÜBER LAGE UND STRUKTUR DER SYNAPSEN IM HERZEN DER SUMPFSCHILDKRÖTE (EMYS ORBICULARIS)

von

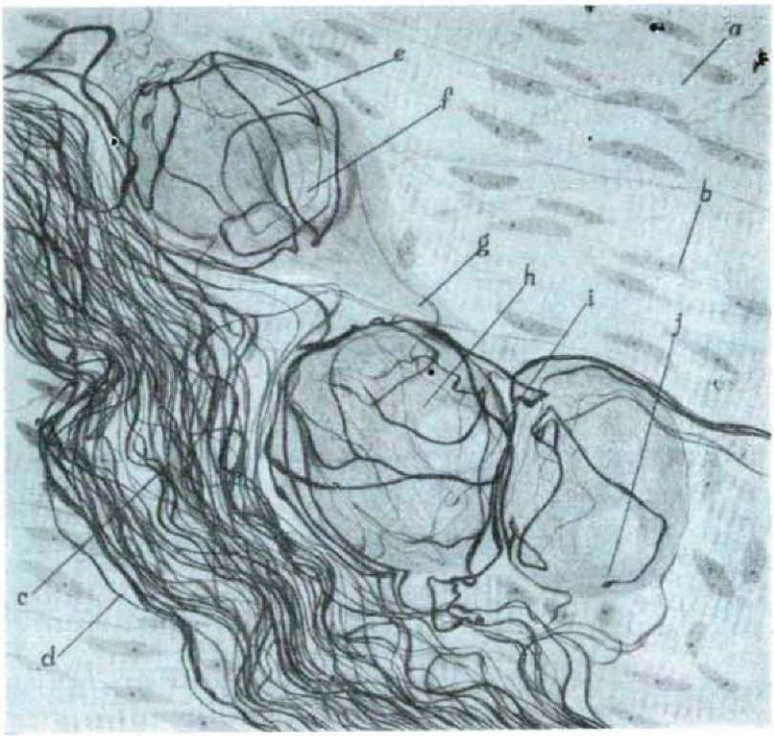
A. ÁBRAHÁM

Institut für allgemeine Zoologie und Biologie der József Attila-Universität Szeged, Ungarn
(Dir.: Prof. Dr. A. ÁBRAHÁM)

Die in das Gebiet der Herzwand entfallenden Synapsen lassen sich in zwei Gruppen teilen. In die eine Gruppe gehören die auf den Nervenzellen Platz nehmenden und in die andere jene, welche die Elemente des *Epikardium*, des *Endokardium* und des *Myokardium* mit dem Nervensystem verbinden. Im Sinne unserer Untersuchungen, die wir mit verschiedenen Versilberungsverfahren durchführten, lassen sich Lage und Struktur der Nervenzellen und der ihnen, sowie dem *Epi-*, *Endo-* und *Myokardium* angehörenden Synapsenformen im Herzen der Sumpfschildkröte (*Emys orbicularis*) folgendermassen umreissen.

Es sind zwei Gruppen von Nervenzellen zu unterscheiden. Der ersten Gruppe lassen sich jene Nervenzellen einordnen, die massenhaft im *Sinus venosus* und in der Vorhofscheidewand vorkommen. Diese Zellen sind gewöhnlich entlang der grösseren Nervenstämme — stellenweise sogar in ziemlich grosser Zahl — anzutreffen. Es sind meistens sphärisch runde, manchmal aber auch oval gestreckte Gebilde. Aus dem Zellkörper tritt stets ein dicker Fortsatz heraus, der in einen benachbarten Nervenstamm eintritt und in diesem in der Regel ungeteilt weiterzieht. Bei diesen eigentümlichen grossen Gebilden handelt es sich unserer Ansicht nach um parasympathische Zellen, die in ihrem Bau weitgehend mit den aus den Vagusganglien, und aus den zerebrospinalen Ganglien im allgemeinen bekannten Zellen übereinstimmen. Diese Zellen, welche typische Bestandteile der Herzwandung der Sumpfschildkröte darstellen, sind ebenso wie jene, die wir aus dem Vorhofseptum des *Rana ridibunda* mitteilten, von eigentümlich geformten, reichen und ziemlich variierenden perizellulären Geflechten umgeben. Die Geflechte haben in sehr zahlreichen Fällen Körbchenform. Im Laufe der sorgfältigen Untersuchung stellt sich jedoch stets heraus, dass es sich hier im wesentlichen nicht um ein geschlossenes Geflecht handelt, sondern um Strukturen, in denen der Verlauf der Fasern genau zu verfolgen ist, und ausserdem ist festzustellen, dass die Fasern an der Zelloberfläche in Gestalt kleiner runder, oder gelegentlich elliptischer Endköpfchen frei endigen. Die Endigungsstelle ist auf der Zelloberfläche scharf umgrenzt. Lichtmikroskopischen Bildern zufolge ist die Lage immer die, dass dort, wo die Faser endigt, sich an der Zelloberfläche eine halbkugelförmige Vertiefung befindet, in der das Ende der Nervenfaser Platz nimmt.

Die die perizellulären Geflechte hervorbringenden Nervenfasern treten aus den nahe den Zellen ziehenden Nervenstämmen hervor, manchmal an der Basis des Zellfortsatzes, am Halsteil der Zelle Spiralen formend. Es kommt aber auch vor, dass die aus dem Nervenstamm an die Zelle herantretende Nervenfaser verzweigt und die Äste gemeinsam das lockere Geflecht um den Körper der Zelle formen. Auch sind Fälle nicht selten, wo der eine Ast der aus dem Stamm heraustretenden Faser die eine, und der andere eine banachbarte Zelle mit einem perizellulären Geflecht versieht. (Abb. 1.)



1. *Emys orbicularis:* Herz. Ganglienzellen vom parasympathischen Typ aus dem *Septum atriorum.* a — quergestreifte Muskelfaser, b — Kern der quergestreiften Muskelfaser, c — Nervenbündel, d — Nervenfaser, e — Nervenzelle, f — Nervenzellkern, g — Nervenzellfortsatz, h — Neurofibrille, i — perizelluläres Körbchen, j — Synapse. BIELSCHOWSKYsches Verfahren. Vergr. 1000×. Photographisch auf die Hälfte verkleinert.

In Verbindung mit den perizellulären Strukturen harren zwei Fragen einer Beantwortung. Die erste Frage lautet: „Woher stammen die Fasern, welche die perizellulären Körbchen zustandebringen?" und die zweite: „Welche Funktion haben diese Nervenfaserkörbchen im Leben des intrakardialen Nervensystems zu erfüllen?"

Gestützt auf die vorgefundenen Verhältnisse und theoretische Überlegungen lässt sich die erste Frage folgendermassen beantworten. Die perizel-

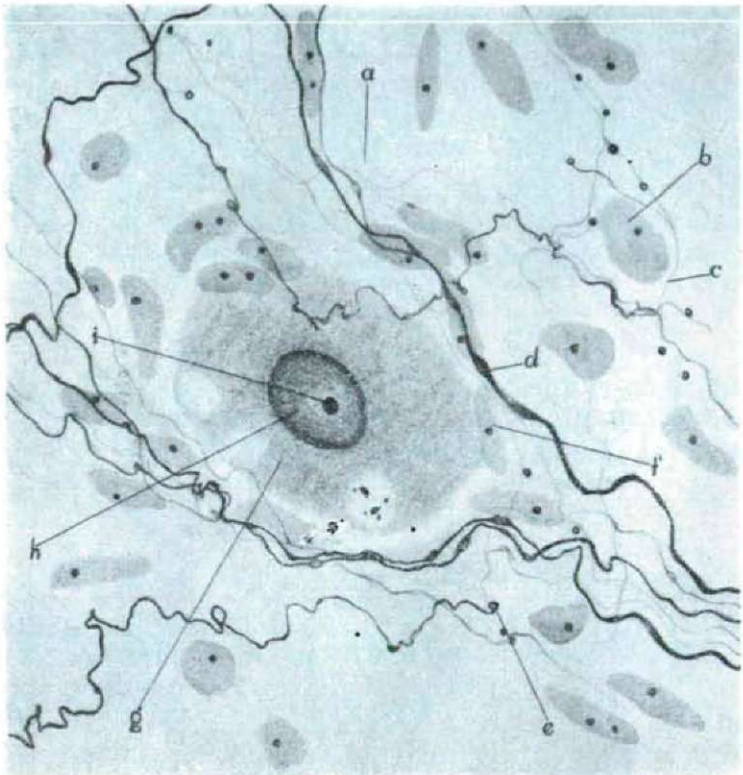
lulären Körbchen können den afferenten Vagusfasern, ebenso aber auch den efferenten Fasern dieses Nerven zugezählt werden. Um eine Antwort auf diese Frage zu erhalten, haben wir bei den Sumpfschildkröten beide zum Herzen ziehenden *N. vagi* durchtrennt, welcher Eingriff sich aber hinsichtlich der Frage als völlig erfolglos erwies, denn die perizellulären Körbchen degenerierten nicht. Daraus könnte geschlossen werden, dass die perizellulären Körbchen formenden Fasern nicht zum Fasersystem des *N. vagus* gehören. Wenn dem aber so ist, woher stammen dann die fraglichen Fasern? Eine possible Antwort auf diese Frage ist, dass wir es hier möglicherweise mit nichts anderem zu tun haben, als mit den Fortsätzen jener parasympathischen Zellen, die entlang den Nervenstämmen, bzw. stellenweise in den Nervenstämmen selbst, Platz nehmen. In diesem Sinne formen die parasympathischen Zellen richtige Ketten im Verlaufe der Nervenstämme und die perizellulären Nervenfaserkörbchen stellen jene vermittelnden Strukturen dar, welche die Zellen zu einer Funktionseinheit zusammenfügen, dabei auch jene miteinbeziehend, die eventuell in grösserer Entfernung voneinander liegen. Für diese Überlegug sind auch die phylogenetischen Grundlagen gegeben, indem die Überreste der Urzellen-Markstränge im Bereich des höchstentwickelten Nervensystems lediglich im vegetativen Nervensystem — insbesondere bei den niederen Wirbeltieren — auffindbar sind.

In der Beurteilung der Herkunft der perizellulären Körbchen taucht auch noch eine andere Möglichkeit auf, und zwar die, dass die Nervenfasern, welche die perizellulären Geflechtssynapsen hervorbringen, aus den intervertebralen Ganglien kommen und in den sensiblen Ästen der ersten Thorakalnerven an die Nervenzellen herantreten. Versuche zur Entscheidung dieser Frage stehen noch aus, doch hoffen wir, in der nächsten Zukunft auch experimentelle Eingriffe in dieser Richtung unternehmen zu können.

Entgegen der in der Literatur oft und vielenorts betonten gegensätzlichen Behauptung sind wir entschieden der Meinung, dass die perizellulären Körbchen echte Synapsen sind, und zwar im Sinne der KIRSCHEschen Nomenklatur Synapsen mit grossem Transmissionsfeld, die entweder aus dem zentralen Nervensystem, oder aber von einem Kettengliede der weiter oben skizzierten Zellkette zum andern die Erregungen weiterleiten.

In die zweite Gruppe gehören jene Nervenzellen, die — wie die meisten der zum sympathischen Nervensystem gehörenden Zellen — viele Fortsätze haben. Solche Zellen kommen vor im Vorhofepikard, sowie im Vorhof- und Kammermyokard. Diese Zellen liegen meistens in reichhaltige Nervengeflechte eingebettet, bzw. bilden Ganglien, kommen aber nicht selten auch als selbständige Zellen im Bindegewebe oder im Myokard zur Beobachtung. Die Fortsätze der Zellen imprägnieren sich nur in den seltensten Fällen ganz scharf. Dann werden deutlich die basal breiten, allmählich und gleichmässig verjüngten und am Ende spitz auslaufenden Fortsätze, die Satellitenzellen und zentral der grosse, runde Kern sichtbar. Zuweilen werden auch die Neurofibrillen wahrnehmbar, die im zellkörper ein Geflecht bilden und in den Fortsätzen parallellaufen. In den meisten Fällen bleiben jedoch die Fortsätze verborgen; das Protoplasma ist homogen, etwas granuliert, die Kernmembran dick und der Nukleolus kompakt. Die Zellen sind nicht von perizellulären Körbchen umgeben. Nervenendigungen kommen gelegentlich auch an diesen Zellen vor, stellen aber dann kleinere Knoten, Köpfchen oder Ringe dar, welche

den Synapsen mit kleiner Transmissionsfläche angehören. Diese Nervenendformationen nehmen in einer kleineren Vertiefung des Zellkörpers Platz. In einer Vertiefung wird in der Regel ein Nervenendknötchen bzw. Nervenendring sichtbar (Abb. 2).



2. *Emys orbicularis:* Herz. Ganglienzelle vom sympathischen Typ aus dem *Epicardium* des Ventrikel. a — Bindegewebe, b — Bindegewebskern, c — Nervenfaser, d — Varix, e — Synapse, f — Satellitenkern, g — Nervenzelle, h — Nervenzellkern, i — *Nucleus* der Nervenzelle. BIELSCHOWSKYsches Verfahren. Vergr. 1600×. Photographisch auf die Hälfte verkleinert.

Die im Gebiete des *Epi-* und *Endokardiums* liegenden Nervenendigungen sind kleinere und grössere Endringe, die die Endigungsformen der stellenweise reichere Geflechtsysteme bildenden glattrandigen, marklosen Fasern darstellen. Diese im wesentlichen Synapsen mit kleiner Transmissionsfläche schliessen sich im Falle beider Bindegewebsmembranen unmittelbar den Bindegewebselementen an, CAJALsche interstitiale Zellen gibt es nicht.

Ob es im *Myokardium* Nervenendigungen gibt oder nicht, wenn ja, welcherart sie sind und wo sie sich befinden, das sind Fragen, mit denen sich

viele und sehr eingehend beschäftigt haben und die auch heute noch alle Untersucher stark beschäftigen, die den Nervenverbindungen des *Myokards* Interesse entgegenbringen. An dieser Stelle soll weder die Literatur der Frage, erörtert, noch die zahlreichen mitgeteilten Ergebnisse und Feststellungen beurteilt werden, ich will lediglich die gefundenen Verhältnisse beschreiben, und zwar um so mehr, als diese hinsichtlich der Beurteilung des Fragenkomplexes von entscheidender Bedeutung sind, muss aber dennoch ganz kurz jener vier Auffassungen Erwähnung tun, die in der Vergangenheit bezüglich der Endigungen der Nervenfasern des *Myokards* im Schrifttum erschienen sind.

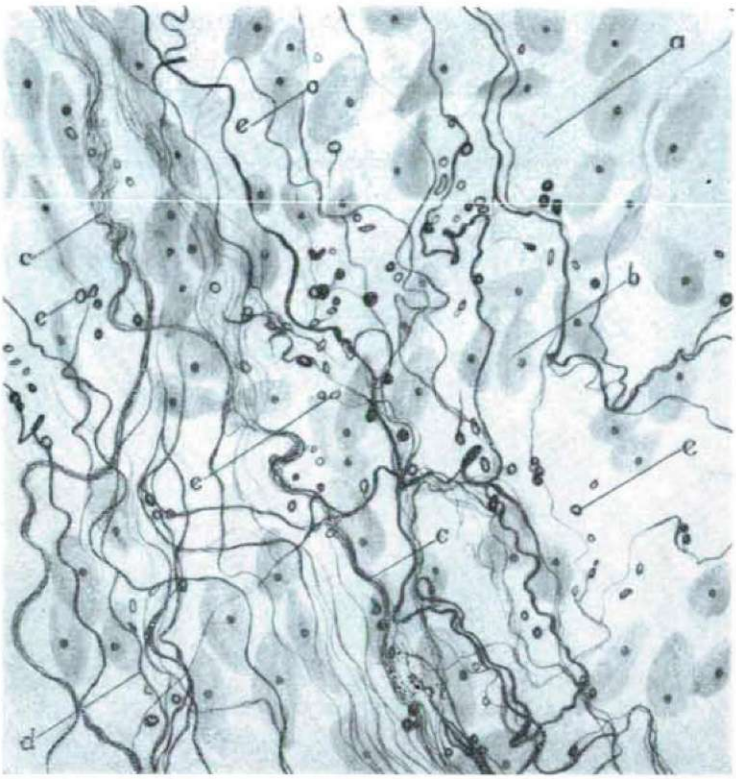
Die erste Konzeption knüpft sich an die Namen von SMIRNOW, LAWRENTJEW und ÁBRAHÁM, danach endigen die efferenten Nervenfasern frei im *Sarkoplasma* der Muskelfasern des *Myokards* ganz nahe des Zellkernes.

Die zweite Auffassung wurde von BOEKE vertreten, der fand, dass nur ein kleinerer Teil der efferenten Fasern in Gestalt von Endköpfchen im Plasma der quergestreiften Muskelzelle endigt. Im grössten Teil der Fälle ist die Lage nämlich die, dass neben den Endkopf-artigen freien Endigungen stets „... ein zartes, aus feinsten, leicht varikösen, immer miteinander anastomisierenden Neurofibrillenzügen aufgebautes Netzwerk vorhanden ist, das sowohl mit den Blutgefässen, wie mit den Muskelfasern zusammenhängt."

Vertreter der dritten Auffassung sind STÖHR und HAHIRO SETO, die jegliche Form der freien Endigung leugnen und die einzige Endigungsformation in dem aus Nervenfasern bestehenden Endnetz, dem Terminalretikulum, erblicken, „... das sich mit Muskelfasern und Blutkapillaren in gleicher Weise plasmatisch verbindet. Elemente aus *Vagus* und *Sympathicus* müssen in diesem Netz enthalten sein und die Tätigkeit der Herzmuskulatur in harmonischer Zusammenarbeit regeln."

Die vierte, von einigen auch heute noch verfochtene Auffassung knüpft sich an den Namen von MEYLING, der — wie in der Arbeit „Cardiovascular Innervation" von MITCHELL zu lesen ist, „... *asserts that the so-called free, loop and bulb endings are artefacts produced by incomplete staining; and he belives the networks formed by the interstitial cells intervene between the efferent fibres and the effector structures.*"

In unseren, aus der Herzwand der Sumpfschildkröte hergestellten Präparaten sind die freien Nervenendigungen einwandfrei sichtbar (Abb. 3). Es sind kleinere und grössere Ring Reifen bzw. Endkölbchen, die im *Myokard* der Herzwand überall ausgezeichnet zutagetreten, im Bereich des Atrio-Ventrikularringes aber in riesiger Menge erscheinen. Da diese Endringe in sämtlichen Anteilen des *Myokards* anzutreffen sind, sind wir entschiedenst der Ansicht, dass die efferenten Fasern in der Herzwand der Sumpfschildkröte frei endigen und in Gestalt von Ringen oder Endköpfchen sich den Muskelfasern anschliessen. In Anbetracht dessen, dass wir ähnliche Erscheinungen bei den Süsswasser-Knochenfischen, bei Fröschen, beim Erdvaran, und bei den Vögeln vorfanden, sind wir — obzwar wir in Bezug auf das *Mykardium* der Säuger über hinreichend positive Daten nicht verfügen — der Meinung, dass im *Myokard* des Wirbeltierherzens sämtliche Fasern in den quergestereiften Muskelzellen bzw. -fasern hypolemmal frei endigen.



3. *Emys orbicularis:* Herz. Synapsen aus der Wand der Ventrikel. a — quergestreifte Muskelfaser, b — Kern der quergestreiften Muskelfaser, c — Nervenbündel, d — Nervenfaser; e — Synapsen. BIELSCHOWSKYsches Verfahren. Vergr. 1600×. Photographisch auf die Hälfte verkleinert.

Zusammenfassung

1. Als Ergebnis der mit den verschiedenen Modifikationen des BIELSCHOWSKYschen Verfahrens am Herzen der Sumpfschildkröte durchgeführten Untersuchungen wird festgestellt, dass die in der Herzwandung befindlichen Nervenzellen zwei Gruppen bilden. In die eine Gruppe gehören die grossen unipolaren Zellen vom parasympathischen Typ und in die andere die multipolaren sympathischen Nervenzellen.

2. Die *Parasympathicus*-Zellen sind von perizellulären Fasergeflechten umgeben, deren Fasern an der Zelloberfläche frei endigen. Diese Geflechte werden als Synapsen aufgefasst.

3. Die sympathischen Nervenzellen besitzen keine perizellulären Nervenfasergeflechte. Auf diesen Zellen befinden sich Endringe, die fallweise in den im Zellplasma befindlichen Vertiefungen Platz nehmen.

4. Die Synapsen des *Epikardiums*, des *Endokardiums* und des *Myokardiums* sind Endringe. Diese nehmen in den beiden ersteren Schichten zwischen den Bindegewebselementen, und in der letzteren hypolemmal in den Muskelfasern Platz.

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ÜBER DIE WIRKUNG VERSCHIEDENER IONEN AUF DAS ISOLIERTE HERZ DER WEINBERGSCHNECKE (HELIX POMATIA)

von

L. ERDÉLYI

Institut für allgemeine Zoologie und Biologie der József Attila Universität Szeged, Ungarn. (Dir.: Prof. Dr. A. Ábrahám)

Über die von verschiedenen Anionen und Kationen auf das isolierte Schneckenherz entfaltete Wirkung finden sich in der Literatur zahlreiche Angaben. So haben sich ARVANITAKI und CARDOT (2), BACHRACH und REINBERG (3), JULLIEN und PEILLON (8, 9, 10, 11), JULLIEN und RIPPLINGER (12, 13), JULLIEN, RIPPLINGER und CARDOT (14), JULLIEN, RIPPLINGER, CARDOT und DUVERNOY (15), RIPPLINGER und JOLY (18), RIPPLINGER, JOLY und CARDOT (19) und andere in mehrerer Hinsicht mit den Na-, K-, Ca- und Mg-Ionen befasst.

Im Gegensatz zu den erwähnten Metallionen ist die Wirkung anderer Ionen weniger untersucht worden. In Bezug auf die Ba-Ionen enthält z. B. die Mitteilung von ACOLAT (1) auf Grund eines einzigen Versuches Angaben: 1 :10 000-fache Verdünnung von $BaCl_2$ wurde als auf das Schneckenherz vollkommen unwirksam befunden, während es in der Verdünnung 1 : 5000 die Herztätigkeit beschleunigte. MOUGEOT und AUBERTOT (17) fanden bei ihren Untersuchungen mit Mineralwässern komplexer Ionenzusammensetzung, dass die verschiedene Mineralien enthaltenden Wässer das Herz vielseitig beeinflussen, indem sie Frequenz-, Amplitüden- und Tonusänderung hervorrufen.

Material und Methoden

Es wurde die Wirkung von $BaCl_2$, $CdCl_2$, und NH_4Cl auf das isolierte Herz der Weinbergschnecken *Helix pomatia* — in 10 ml fassenden Organgefässen aufgehängt — untersucht (s. Abb. 1). Das Aufhängen der Präparate erfolgte unter Berücksichtigung der theoretischen Feststellungen von BLANC, JULLIEN und MORIN (6), WILLEMS (20, 21) und WOLVEKAMP jun. (22), und Vermittlung von zum Vorhof und zur Kammerspitze geschnittener, kleiner perikardialer Gewebsstückchen. Bei dieser Aufhängungsweise war die Kammerspitze der fixe Punkt, und der Schreibhebel war der Vorhofspitze angeschlossen. Die Herzfunktionskurven wurden an der langsam rotierenden Kimographenwalze mit Tinte aufgezeichnet. Während der Versuchsdauer wurde das Organgefäss mit Hilfe eines Ultrathermostats bei 27° gehalten und auch für Sauerstoffversorgung des Gefässes Sorge getragen. Die „*Helix*-Ringer-Lösung" wurde unter Berücksichtigung der Lymphanalyse von BINET, LÉON und PERLÉS (5), sowie JULLIEN, ACOLAT, RIPPLINGER, JOLY und VIEILLE-CESSAY (7) auf das optimale Niveau eingestellt.

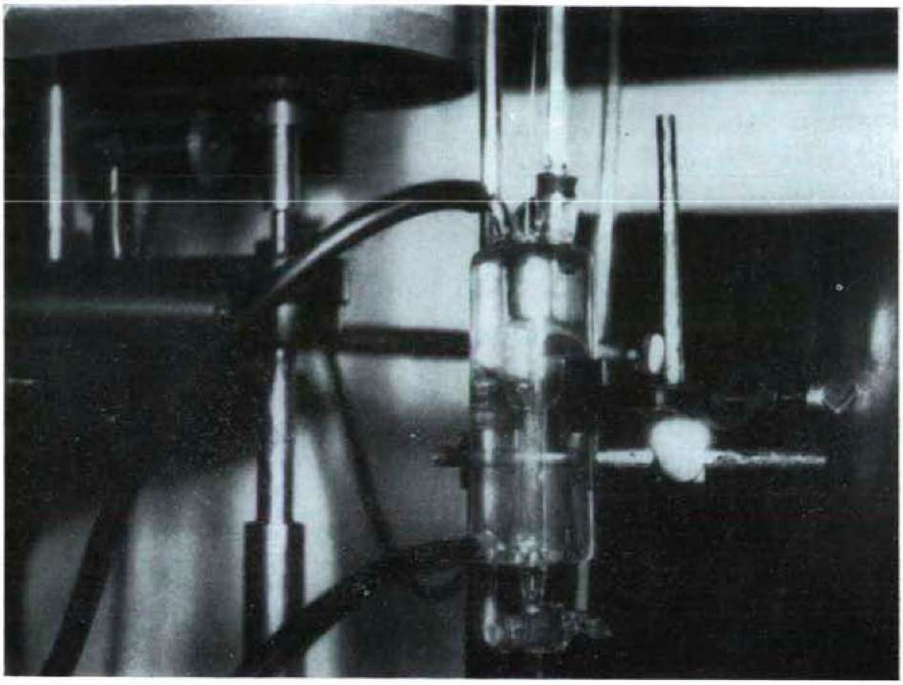


Abb. 1. Das zur Untersuchung der isolierten Schneckenherzen benutzte Organgefäss mit den angeschlossenen Zubehören.

Untersuchungsergebnisse

Das $BaCl_2$ bewirkt in Gaben unter 0,004 g/10 ml Helix-Ringerlösung im wesentlichen die gleichen Ergebnisse, wie sie schon von ACOLAT (1) beschrieben wurden. Im Bereich von 0,004—0,08 g dagegen war bei Anwendung jeglicher kleinen Dosis — oder wenn der angegebene Höchstwert durch Kumulation der niedrigen Komponenten erreicht wurde — eine charakteristische Wirkungsänderung festzustellen, die sich in einem Anstieg des Amplitudo und in einer Frequenzverminderung bemerkbar machte (s. Tafel, Abb. 1). Die Entwicklung der beschriebenen Wirkung wurde durch die Ionenzusammensetzung der angewandten *Helix*-Ringerlösung beeinflusst, war aber auch noch bei Ionen- Proportionen auslösbar, wo sonst ein starkes Nachlassen der Herzfunktion zu verzeichnen war. Wird das $BaCl_2$ in 0,004—0,2 g/10 ml *Helix*-Ringerlösung-Dosen portionenweise gleichzeitig verabreicht, kommt es zum Barium-Spasmus des Herzmuskels und es wird eine homologe Reaktion erhalten, wie im Falle der glatten Muskulater des Darmes (s. MINKER und KOLTAI, 16). Bei der niedrigeren Dosis (0,008 g/10 ml. Helix-Ringerlösung) ist die Tonusänderung eine ziemlich milde und auch die automatische Herzbewegung wird nicht geschädigt (Abb. 2 A). Bei der höheren Dosis dagegen ist die Tonusänderung eine intensivere und auch die automatische Herzmotilität bleibt nur entlang dem aufsteigenden Schenkel der Kurve erhalten, wo sie beschleunigt ist, um dann später stillzustehen (Abb. 2 B). Den Bariumkrampf vermag das Papaverin nicht zu lösen.

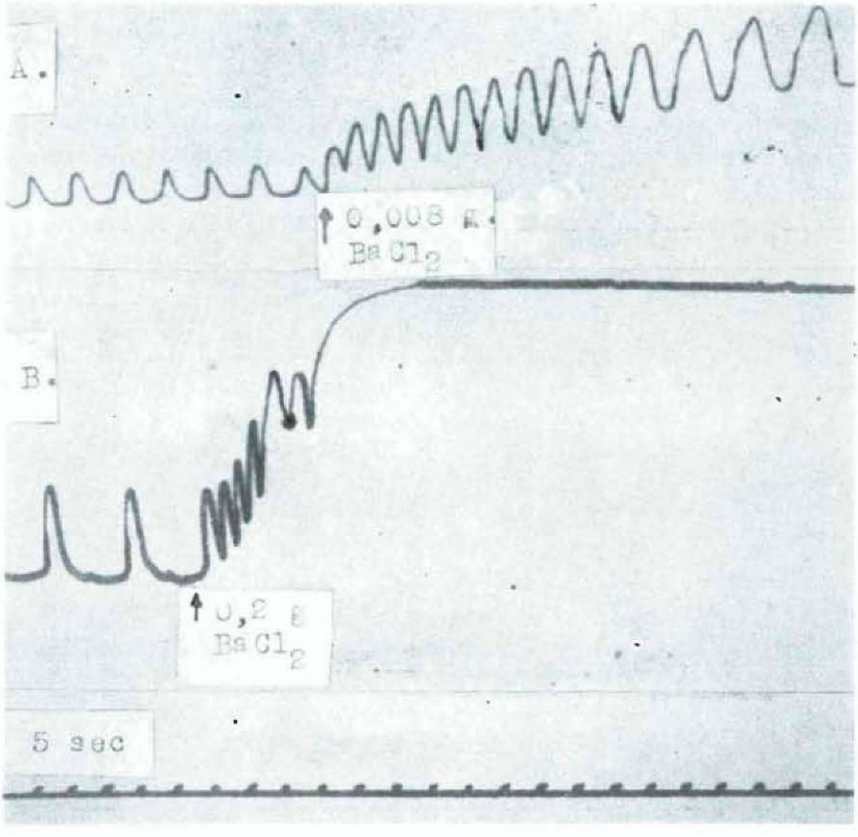
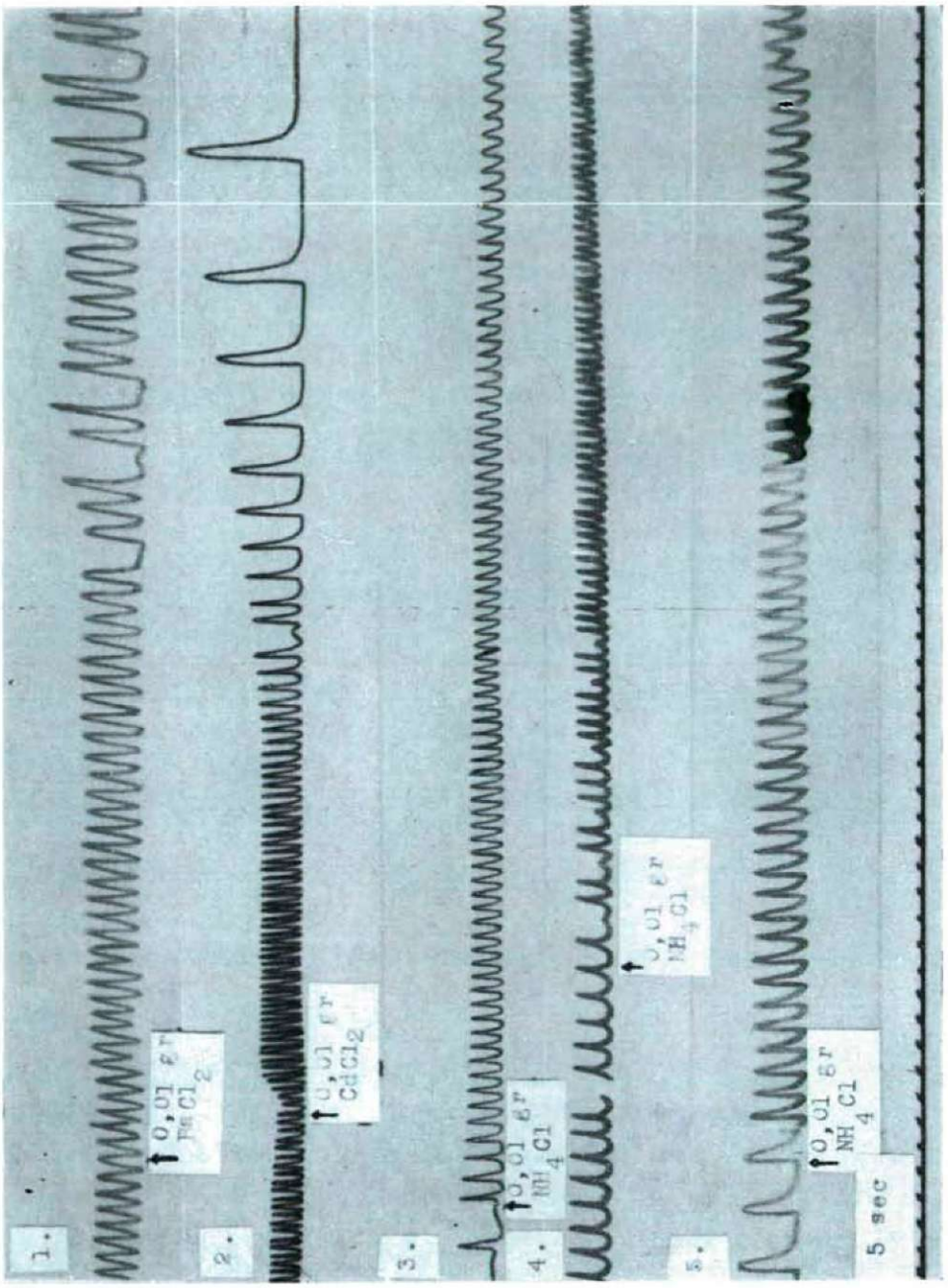


Abb. 2. Wirkungskurve des $BaCl_2$. A: leichte Tonusänderungen, B: starke Tonusänderungen.

Das $CdCl_4$ bewirkt (am ausgesprochensten in Gaben von 0,01 g/10 ml *Helix*-Ringerlösung) ähnlich wie das $BaCl_2$ starke Amplitüdenerweiterung und allmählich zur Entwicklung gelangende Frequenzverminderung (s. Tafel, Abb. 2). Besonders schnell manifestiert sich die $CdCl_2$-Wirkung, wenn das gleiche Präparat vorher auch mit $BaCl_2$ behandelt wurde.

NH_4Cl wirkt (am ausgesprochensten in Gaben von 0,01—0,06 g/10 ml *Helix*-Ringerlösung) entgegengesetzt wie $CdCl_2$ und $BaCl_2$: es zeitigt deutliche Amplitüdenverminderung und lässt die Frequenz unverändert oder steigert sie (s. Tafel, Abb. 3). Wird das NH_4Cl nach dem $BaCl_2$ oder $CdCl_2$ angewandt, so kommt am Präparat die NH_4Cl-Wirkung zur Geltung (s. Tafel, Abb. 4 und 5), während bei gleichzeitiger Untersuchung mit dem $BaCl_2$ oder $CdCl_2$ die Wirkung der letzteren Ionen dominiert.

Aus den Mittellungen von BEAUVALLET (4), sowie MINKER und KOLTAI (16) geht hervor, dass die spontanen Bewegungen des Schneckendarmes durch NaCl, KCl, $CaCl_2$, $MgCl_2$, CdJ_2 und NH_4Cl herabgesetzt oder aufgehoben werden können, während $BaCl_2$ sie stimuliert. In Anbetracht dieser Befunde kann letzten Endes auf Grund der bisher durchgeführten Untersuchungen fest-


1.
2.
3.
4.
5.
0,01 er
MgCl2
0,01 er
CdCl2
0,01 er
NH4Cl
0,01 er
NH4Cl
0,01 er
NH4Cl
5 sec

gestellt werden, dass die antagonistische Wirkung von $BaCl_2$ und NH_4Cl auch am Herzen zu beobachten ist, während ein Antagonismus zwischen $BaCl_2$ und $CdCl_2$ im Falle des Herzens nicht besteht.

Zusammenfassung

Die am isolierten Herzen von *Helix pomatia* erhaltenen Ergebnisse lassen sich kurz folgendermassen zusammenfassen:

1. $BaCl_2$ und $CdCl_2$ bewirken Amplitüdenvergrösserung und Frequenzherabsetzung.
2. NH_4Cl verursacht im Gegensatz zum $BaCl_2$ und $CdCl_2$ Amplitüdenverminderung und Frequenzbeschleunigung.
3. Die erhobenen Befunde zeigen, dass — ähnlich wie beim Darm — auch im Falle des Herzens ein Antagonismus zwischen $BaCl_2$ und NH_4Cl festzustellen ist, während ein solcher zwischen $BaCl_2$ und $CdCl_2$ nicht besteht.

Erklärung der Tafeln

1. Wirkungskurve des $BaCl_2$. $BaCl_2$ verursacht Amplitüdenvergrösserung und setzt die Frequenz herab.
2. Wirkungskurve des $CdCl_2$. $CdCl_2$ bewirkt Amplitüdenerweiterung und allmähliches Nachlassen der Frequenz.
3. Wirkungskurve des NH_4Cl. NH_4Cl setzt die Amplitüden herab und steigert die Frequenz.
4. Wirkungskurve des NH_4Cl. Das Präparat war zunächst mit 0,01 g/10 ml *Hellix*-Ringerlösung $BaCl_2$ und nach Auswechseln der Ringerlösung mit NH_4Cl behandelt worden.
5. Wirkungskurve des NH_4Cl. Das Präparat war zunächst mit 0,01 g/10 ml *Hellix*-Ringerlösung $CdCl_2$ und nach Auswechseln der Ringerlösung mit NH_4Cl behandelt worden.

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DIE MIKROSKOPISCHE INNERVATION DES DARMKANALS DER KAULQUAPPEN

von

I. HORVÁTH

Institut für allgemeine Zoologie und Biologie der József Attila Universität Szeged, Ungarn
(Dir.: Prof. Dr. A. ÁBRAHÁM)

Im Anschluss an die früheren vergleichenden neurohistologischen Untersuchungen der einzelnen Darmstrecken ausgewachsener Frösche wurden in der vorliegenden Arbeit die Innervationsverhältnisse im Darmtrakt von Kaulquappen studiert. Die Bewegungen des Darmkanales werden — ausser von den beiden bekannten Nervengeflechten — auch von zentral-vegetativen Nervenfasern beeinflust. Aufschluss über den Ursprung dieser Fasern wurde aus den Nervendurchtrennungsversuchen erhalten (7). Die vorliegende Mitteilung bringt einige Beiträge zur näheren Erkenntnis der Innervation des Darmkanals zuf Grund neurohistologischer Untersuchungen an Kaulquappen.

Material und Methoden

Aus den Erdgruben in der Umgebung von Szeged zur Zeit der Froschlaiche wiederholt gesammelte Kaulquappen wurden auf Grund ihrer äusseren morphologischen Merkmale und der Struktur ihrer Chromatophoren systematisch geordnet. Sie gehörten folgenden Arten an: *Rana ridibunda, Pelobates fuscus fuscus* und *Bufo viridis viridis.* Nach Fixierung in 10%igem neutralem Formalin wurden neurohistologische Präparate nach BIELSCHOWSKY—ÁBRAHÁM (2), BIELSCHOWSKY—GROS (3) und AGDUHR (11) hergestellt und die Azetylcholinesteraseaktivität mit der GEREBTZOFF—COUPLAND—HOLMESschen Modifikation (6) des KOELLE—FRIEDENWALDschen Verfahrens (9) untersucht.

Die Innervation des Darmkanals

Vom Verdauungstrakt der den obigen drei Froscharten angehörenden Kaulquappen wurde der Magen und der mehrfach gewundene Dünndarmabschnitt untersucht. Selbst die histologischen Schichten des Magens waren von einer Feinheit, dass Totalimprägnation als das geeigneteste Verfahren erschien. Die Magenschnitte wurden im Gefriermikrotom hergestellt, gingen aber infolge des lockeren Gefüges der die Nervenelemente enthaltenden Gewebe mehrfach zugrunde, so dass ich die bezüglich der Innervation leichter bewertbaren Präparate aus den totalimprägnierten Darmabschnitten erhielt. Beim *Pelobates*

werden zwischen den einige Zellen hohen zirkulären und longitudinalen glatten Muskelschichten der *Tunica muscularis* des Magens — ebenso wie bei ausgewachsenen Fröschen — Nervenstämme wahrnehmbar, die grösstenteils aus dünnen marklosen Fasern bestehen und nur vereinzelt auch dickere Fasern enthalten. Bei den beiden anderen Arten weisen die Nervenfasern des Magens Ähnlichkeit mit den im *Duodenum* gefundenen Nervenfasern auf. Zwischen der inneren zirkulären und der äusseren longitudinalen, aus 1—2 glatten Muskelzellen bestehenden Schicht der *Tunica muscularis* des Dünndarms werden in mehr-minder grosser Zahl nur einzelnstehende Fasern sichtbar, von denen die dickeren regelrecht in caudo-cranialer Richtung verlaufen (Abb. 1) und stellen-

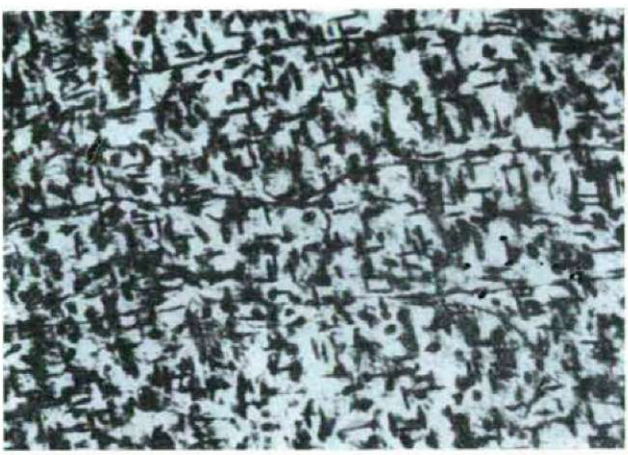

Abb. 1. *Rana ridibunda* (Kaulquappe): Parallel verlaufende dickere Nervenfasern im *Duodenum*. AGDUHR-Methode, Mikroaufnahme, x 250.

weise Fibrilliertheit aufweisen. In ihrem Verlauf entspringen nach dichotomischer Teilung dünnere Seitenäste, die in den zwischen den dickeren Fasern liegenden Gebieten quer verlaufen und — verjüngt — ohne Endringe zwischen den Zellen endigen. Die Nervenfasern gelangen durch das den Darmabschnitten verbundene Mesenterium zum Darm. Der Darmkanal ist noch sehr arm an Blutgefässen, in geringer Zahl sind sie in der Nähe des dem Darm anliegenden Mesenterium zu beobachten. In einem Falle konnte ich bei einer *Pelobates fuscus*-Kaulquappe runde Zellen beobachten, die meines Erachtens amöboide Bewegungen vollziehende, in Entwicklung befindliche Nervenzellen gewesen sein dürften (12). (Abb. 2), aus denen wahrscheinlich später in den Darmabschnitten bei ausgewachsenen Tieren gut zu unterscheidende Nervenzellen von einem DOGIEL-Typ hervorgehen (4). Ausserdem sind noch im *Duodenum* Nervenzellen anzutreffen, die kleinere oder grössere Gruppen bilden (5), (Abb. 3), und deren runder Kern randständig gelagert ist. Bei den im *Mesenterium* gefundenen Zellen füllt der Kern noch fast die ganze Zelle aus und hat nicht so entschieden runde Form wie in den an der Pylorus-Duodenumgrenze befind-

lichen Zellen. Nach meiner Ansicht dürften diese beiden Zelltypen nach ihrer Differenzierung die Grundform der DOGIEL I.- und DOGIEL II.-Zellen darstellen. Zur näheren Entscheidung der Frage sind neurohistologische Untersuchungen bei entwickelten, über einen degenerierenden Schwanz verfügenden Fröschen nötig, darüber hinaus möchte ich meine Forschung auch auf die Erkennung des *Truncus sympathicus* ausdehnen.

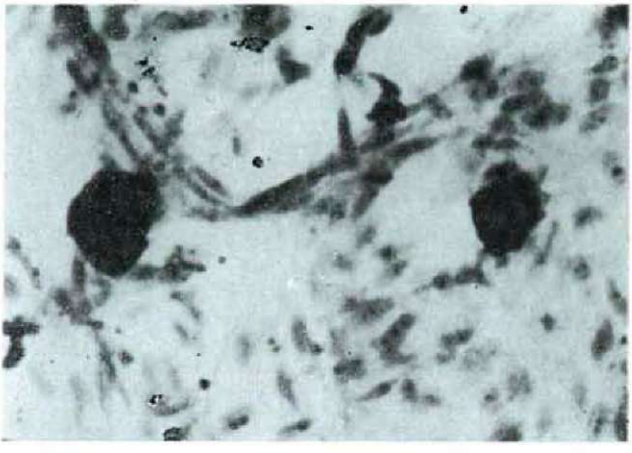

Abb. 2. *Pelobatus fuscus* (Kaulquappe): In Teillung begriffene Nervenzelle im *Mesenterium* des Darmes. AGDUHR-Methode Mikroaufnahme, x 650.

Abb. 3. *Rana ridibunda* (Kaulquappe): Kleinere Gruppen bildende runde Nervenzellen an der Grenze zwischen *Pylorus* und *Duodenum*. AGDUHR-Methode. Mikroaufnahme, x. 945.

Die Azetylcholinesteraseaktivität des Darmkanals

Die zu den Untersuchungen verwendeten Darmabschnitte der drei Kaulquappenarten wurden als Totalpräparate nach den erwähnten Methoden (6—9) unter Benutzung der auf pH 5 eingestellten Inkubationslösungen aufgearbeitet. Zur Sonderung der beiden Cholinesterasen habe ich neben der Azetylcholinjodidinkubation auch die Butyrilthiocholininkubation benutzt und parallel ausserdem einen Teil der Darmabschnitte mit einer 10^{-5} M spezifisch hemmenden Diisopropyl-Fluorophosphatlösung vorinkubiert (8). In den mit Azetylthiocholin inkubierten, sowie den mit Diisopropyl-Fluorophosphat vorbehandelten und mit Azetylthiocholin inkubierten Magen- und Duodenumpräparaten war entlang der Nervenfasern eine Aktivität (Dunkelbraunfärbung) festzustellen (Abb. 4). Bei den mit Butyrilthiocholin inkubierten, sowie den mit Diisopropyl-

Abb. 4. *Pelobates fuscus* (Kaulquappe): Azetylcholinesteraseaktivität im *Plexus myentericus* des *Ventriculus*. GEREBTZOFF—COUPLAND—HOLMESSche Medifikation des KOELLE—FRIEDENWALDschen verfahrens. Mikroaufnahme, x 210.

fluorophosphat vorbehandelten + mit Butyrilthiocholin inkubierten Präparaten war dagegen keine Spur einer Aktivität festzustellen. Die Auswertung der Präparate ergibt somit, dass im Darmkanal der Kaulquappen dieser untersuchten Froscharten spezifische Cholinesterase vorkommt, und bei einigen der erwähnten Zelltypen ebenfalls eine echte Cholinesteraseaktivität zur Beobachtung gelangte. Im Darmkanal der ausgewachsenen Exemplare dieser Arten konnte — besonders bei einem Teil der die Gefässe begleitenden Nervenfasern und den DOGIEL I- und DOGIEL II-Zellen — eine Aktivität beobachtet werden. Vergleicht man diese Befunde mit den von MÜLLER bei Embryonen von Wirbeltieren durchgeführten Untersuchungen — wonach aus dem zentralen Vagus-

system durch den Nervenstamm des *Vagus* Nervenzellen in die intramuralen Darmplexuse eintreten können (1, 10), so können die bei den von mir untersuchten Kaulquappen eine Cholinestaraseaktivität zeigenden Nervenzellen als vom *Vagus* stammend betrachtet werden.

Zusammenfassung

Die Ergebnisse der an den Kaulquappen der drei Froscharten (*Rana ridibunda, Pelobates fuscus* und *Bufo viridis*) durchgeführten neurohistologischen und Cholinesteraseuntersuchungen lassen sich wie folgt zusammenfassen:

1. Zwischen den beiden Muskelschichten der *Tunica muscularis* kommen im Magen neben dünnen, marklosen Fasern im Nervenstamm auch einige dickere Nervenfasern vor.

2. Im Dünndarm finden sich in caudo-cranialer Richtung parallellaufende Nervenfasern, die sich dichotom verzweigen und zwischen den Zellen endigen.

3. Im *Mesenterium* und im *Plexus mesentericus* sind zwei verschiedene, gut voneinander zu unterscheidende, noch fortsatzlose, undifferenzierte Nervenzellentypen zu beobachten.

4. An einigen Nervenzellen der Darmstrecken und entlang der Nervenfasern war eine spezifische Cholinesteraseaktivität festzustellen.

Schrifttum

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EIN BEITRAG ZUR STRUKTUR UND MIKROSKOPISCHEN INNERVATION DER HARDERSCHEN DRÜSE DER VÖGEL*

von

A. STAMMER

Institut für Allgemeine Zoologie und Biologie der József Attila-Universität Szeged, Ungarn
(Dir.: Prof. Dr. A. ÁBRAHÁM)

An der hinteren ventralen Oberfläche des Augapfels findet sich bei allen Vögeln die zum dritten Augenlid, der Nickhaut *(Membrana nictitans)*, gehörende Hardersche Drüse, deren Form und Grösse überaus verschieden ist. Betreffs ihrer anatomischen Erscheinung finden sich genaue Angaben in dem Handbuch von BOLK (4), PLATE (8), KÜKENTHAL (12). — Aus den Arbeiten von MAC LÉOD (6), PETERS (7), SLONAKER (9) und HOFFMANN (5) sind auch Informationen bezüglich der Ontogenese, der histologischen Struktur der Drüse und der Beschaffenheit ihres Sekretes zu entnehmen, über ihre Innervation ist dagegen nichts bekannt. Daher ist das Bestreben, ihre mikroskopische Innervation gründlich kennen zu lernen, berechtigt, und zwar um so mehr, als die physiologisch entschiedene, doppelte Innervation der Drüsen in ihren morphologischen Grundlagen auch bis heute von keinem einzigen Forscher hat überzeugend bewiesen werden können. Auf Grund unserer bisherigen vergleichenden Untersuchungen* über die Innervation des Auges scheinen uns die makroskopischen und mikroskopischen Nervenverbindungen der Harderschen Drüse der Vögel zur Untersuchung der Frage besonders geeignet.

Material und Methoden

Bei der Auswahl des Untersuchungsmaterials waren die verschiedene Lebensweise, sowie die Abweichungen in anatomischer Hinsicht und in der Qualität des Sekrets die leitenden Gesichtspunkte. Es wurden die Harderschen Drüsen der folgenden Vögel untersucht: Von den Hausvögeln *Columba domestica, Anas domestica, Meleagris gallopavo,* von den Raubvögeln *Buteo lagopus, Circus pygarus* und *Falco cherrug,* von den Wasservögeln *Larus ridibundus, Anas platyrhyncha, Fulica atra, Nycticorax nycticorax* und von den Singvögeln *Alauda arvensis* sowie *Turdus merula.* Die in 10%igem Formalin fixierten Drüsen wurden zu 10—20 μ dicken Schnitten aufgearbeitet und mit den Modifikationen der Bielschowskyschen Methode von ÁBRAHÁM, CAUNA, JABONERO und GROS—SCHULTZE imprägniert und an den 10—15 μ dicken Schnitten von Tauben auch die Cholinesteraseaktivität der Drüse nach Gerebtzoff untersucht.

* Die vergleichende Untersuchung der Innervation des Auges ist ein mit Herrn Professor ÁBRAHÁM gemeinsam bearbeitetes Thema.

Makroskopische Nervenverbindungen

Die Nervenversorgung der Harderschen Drüse ist nicht entschieden. Sie liegt dort, wo das reich verzweigende System der das Auge versehenden vier Gehirnnerven *(Nervus oculomotorius, trochlearis, trigeminus* und *abducens)* in Erscheinung tritt, welches auch im binokularen Präparier-Mikroskop schwer zu verfolgen und bei den einzelnen Arten verschieden ist. Erschwert wird die klare Sicht ferner dadurch, dass auch sie die *Arteria ophthalmica* auf diesem Gebiet ihre Zweige abgibt und die Verzweigungen ihres *Ramus temporalis* sehr oft entlang der Nervenfasern ziehen. CORDS (2), der sich mit der Anatomie der Gehirnnerven der Vögel befasst, erwähnt keine in die Hardersche Drüse eintretende Nerven. SLONAKER (9) dagegen fand beim Sperling, dass aus dem *Ramus inferior* des *Nervus oculomotorius,* und zwar aus dessen einem, im *Musculus obliquus inferior* verlaufenden Aste, der Nerv der Harderschen Drüse hervorgeht. Diesen Befund können wir nicht bekräftigen. Bei mehreren Vogelarten haben wir den *Ramus inferior* des *Nervus oculomotorius* bis zuende verfolgt, der — namentlich bei grösseren Vögeln — auch mit freiem Auge gut wahrnehmbar ist. Es ist schwer vorstellbar, dass ihm ein so feiner Seitenast entspringen und zu der relativ grossen Harderschen Drüse ziehen sollte, dessen Erkennung Schwierigkeiten macht. Allerdings ist fast stets ein an den aus dem Tor der Drüse heraustretenden Drüsenleiter hinanschwenkendes dünnes, blasses Ästchen zu beobachten, welches meistens vom Oculomotoriusast zu verfolgen ist, das wir aber für ein Blutgefäss halten, welches zweifellos ein teilweiser Träger der Nervenversorgung der Drüse, nicht aber ein Ast des *Oculomotorius* ist, wie auch die mikroskopische Untersuchung es bekräftigt. Demnach erhält die Hardersche Drüse der Vögel keinen makroskopisch nachweisbaren Nervenast und die Entscheidung der Frage ist lediglich von mikroskopischen Untersuchungen zu erwarten.

Mikroskopische Innervation

Obzwar die Hardersche Drüse mit freiem Auge sichtbare Nervenäste nicht erhält, ist ihre mikroskopische Nervenversorgung dennoch sehr reich zu nennen. Zur Erkennung dieser reichen Innervation musste der Ursprung der Nervenfasern, die Form ihrer Endigungen und die Abweichung zwischen den Arten klargestellt werden.

Der Ursprung der Nervenfassern

Bei der Untersuchung des Ursprunges der Nervenfasern ist festzustellen, dass sie zum grössten Teil jenen Ganglien entstammen, welche sich in ziemlich grosser Zahl und Form im umgebenden Bindegewebe befinden, während der übrige Teil dem reichen Geflecht der in die Drüse eintretenden Arterie entspringt. Die umfangreichsten Ganglien nehmen im Eingang der Drüse, wo der Hauptausführungsgang und die Hauptarterie zusammentreffen, Platz, doch sind mehr-minder grosse Ganglien in der Bindegewebshülle überall auffindbar und — da gewöhnlich in der Nähe der Ganglien auch eine Arterie anzutreffen ist — hat es den Anschein, als ob die Nervenzellen die in die Drüse eintretenden

und in der Kapsel reich verzweigenden Arterienäste verfolgen würden. Mehrfach sahen wir neben dem in der Drüsensubstanz verlaufenden Blutgefäss auch 2–3 Nervenzellen liegen. Von den Ganglien der Drüse haben die im Eingang liegenden unregelmässige Gestalt, während die in der Kapsel gelegenen länglich-elliptische Gebilde mit ausnahmslos Sympathicuscharakter sind (Abb. 1). Die

Abb. 1. *Columba domestica:* Ganglion in der Kapsel der Harderschen Drüse. a — Nervenstamm, b — multipolare Nervenzelle, c — Zellfortsatz, d — Zellkern, e — Pericytakern, f — Nervenfaser, g — Bindegewebskern, h — Drüsensubstanz. BIELSCHOWSKY—ÁBRAHÁMsches Verfahren. Vergrösserung 300×, photographisch auf die Hälfte verkleinert.

Ganglienzellen sind multipolärer Art, ihre Fortsätze nicht zahlreich (3–5), sie können dem Dogiel II.-Typ zugerechnet werden, da alle ihre Fortsätze lang sind und Nervenstämme formend — in die Drüsensubstanz eindringen. Die Nervenstämme enthielten mitunter auch einzelne Nervenzellen. Die Zellen der Ganglien zeigten versilbert die gleiche Tönung, Synapsen wurden in den Ganglien in kleinerlei Form sichtbar, und in den die Ganglien verlassenden Nervenstämmen fanden sich nur sehr schlanke Fasern.

In der Wand der in die Hardersche Drüse eintretenden Hauptarterie kommen die übrigen, die Drüse versorgenden Nervenfasern an. Das Nervengeflecht ist auch entlang der in der Kapsel und in der Drüsensubstanz immer mehr ver-

zweigenden Arterienäste reich, da sich diesen Geflechten auch die aus den Ganglien kommenden Nervenstämme anschliessen. Sämtliche Schnitte beweisen, dass die reichhaltige Nervenversorgung der Drüsensubstanz den in der Wand der Arterien, bzw. entlang derselben ziehenden Nervenstämmen entsammen (Abb. 2). Beachtenswert ist, dass im Geflecht der Wand der eintretenden Arterie

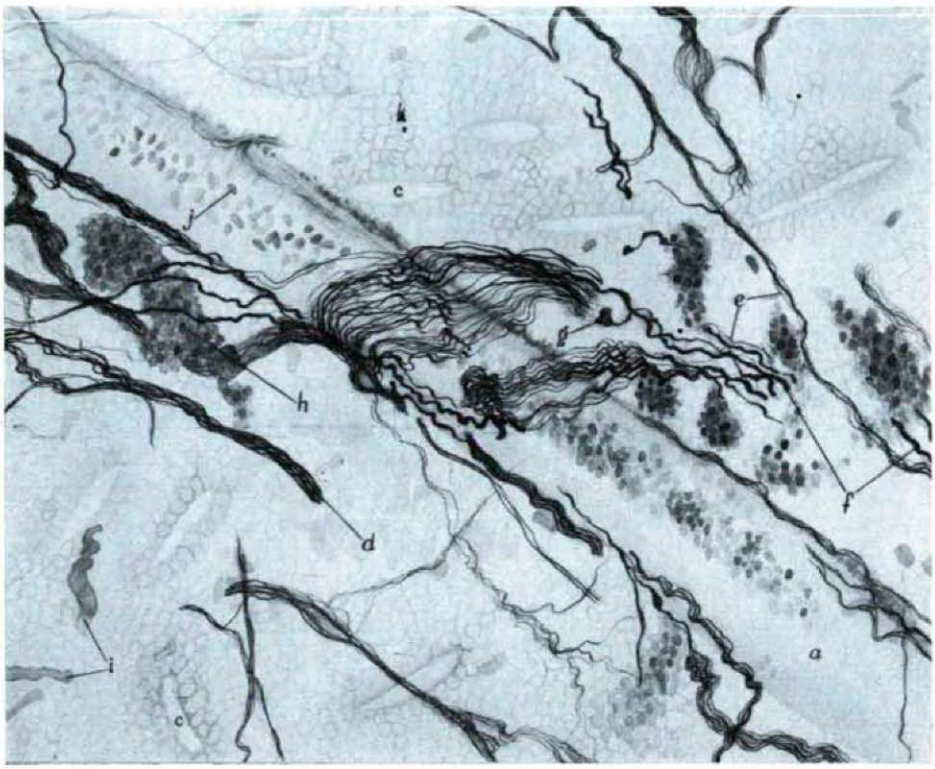


Abb. 2. *Circus pygarus:* Nervengeflecht neben der Hauptarterie in der Drüsensubstanz. a — Arterie, b — Drüsenzellen, c — Ausführungsgang, d — Nervenstamm, e— dünne Nervenfaser, f — dicke Nervenfaser, g — Endlamelle, h — Venen, i — Pigment, j — Erythrocyten. BIELSCHOWSKY—ABRAHÁMsches Verfahren. Vergrösserung 300×, photographisch auf die Hälfte verkleinert.

dünne und dicke Fasern gleichermassen anzutreffen sind. Die dicken Fasern treten nach unseren Beobachtungen nie von den Blutgefässen zwischen die Endkammern der Drüse hinaus.

Endigungen

Die entlang der Arterien in die Drüsensubstanz eindringenden Nervenstämme ziehen in Richtung der Endkammern und formen — diese kreisförmig umgebend — ein Endgeflecht. Besonders gut zu studieren sind die Endgeflechte dort, wo oberflächliche Anteile der Endkammern im Schnitt sichtbar werden

(Abb. 3).* Hier ist dann deutlich zu beobachten — im ganzen Querschnitt werden nur 1—2 Fasern um die Endkammern sichtbar —, dass an der Wand der Endkammern zahlreiche Nervenfasern das Endgeflecht hervorbringen. In den terminalen Fasern sind häufig kleine längliche Varikositäten (Abb. 3, e) anzutreffen. In gut imprägnierten Schnitten wird auch einwandfrei sichtbar, dass die Endfasern ihre Selbständigkeit auch in dem die Endkammern umgebenden Endgeflecht bewahren, und wir haben in keinem einzigen Falle ein Endnetz *(Terminalretikulum)* vorgefunden, wie sie um die Endkammern der Speicheldrüsen beschrieben worden sind (11). Von den zirkulären Terminalfasern schwenken einige Endäste — im Winkel von 90° — zwischen die Zellen der Endkammern (Abb. 3, d). Diese zwischen den Drüsenzellen verlaufenden Endfasern halten wir für die am tiefsten eindringenden Nervenelemente. Dass Endfasern auch in das Plasma der Drüsenzellen eingetreten wären und so innigste Verbindungen hergestellt hätten, war im Lichtmikroskop nicht zu beobachten. Die meisten der in die Drüse eintretenden Nervenfasern — sämtliche dünne Fasern — endigen im Endgeflecht. Am deutlichsten zeigt sich dies im Gebiet um die Endkammern, doch sind Spuren solcher Geflechte auch an der Wand der Ausführgänge wahrnehmbar. Die grössten Ausführgänge und die grössten

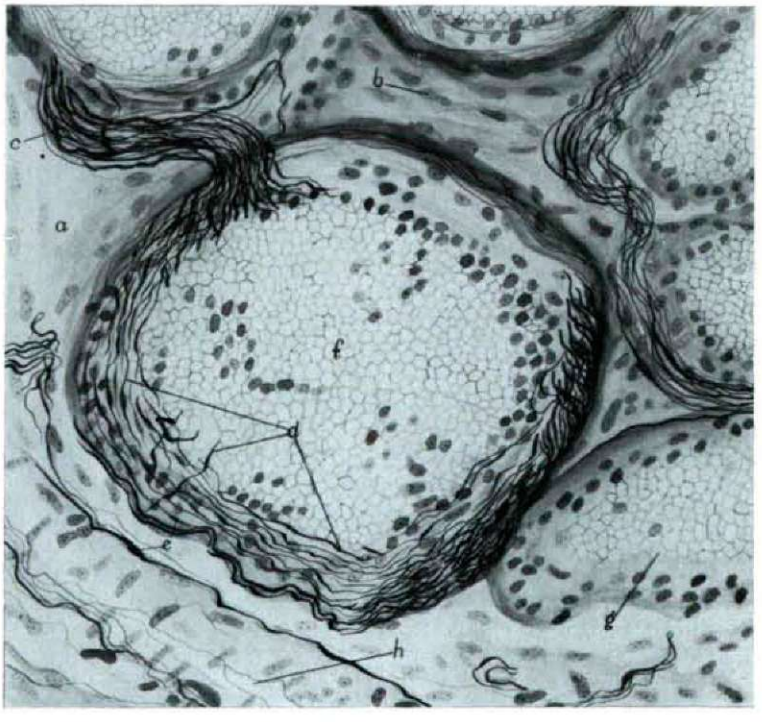


Abb. 3. *Falco cherrug:* Perialveoläres Endgeflecht. a — Bindegewebe, b — Bindegewebskern, c — Nervenstamm, d — Endfaser, e — Varikosität, f — Drüsenzellen, g — alveoläre Endstücke, h — Arterie mit ihrem Nervengeflecht. BIELSCHOWSKY—ABRAHÁMsches Verfahren. Vergrösserung 600×, photographisch auf die Hälfte verkleinert.

* Die Zeichnungen wurden von unser Zeichnerin ELISABET DÁNOS hergestellt.

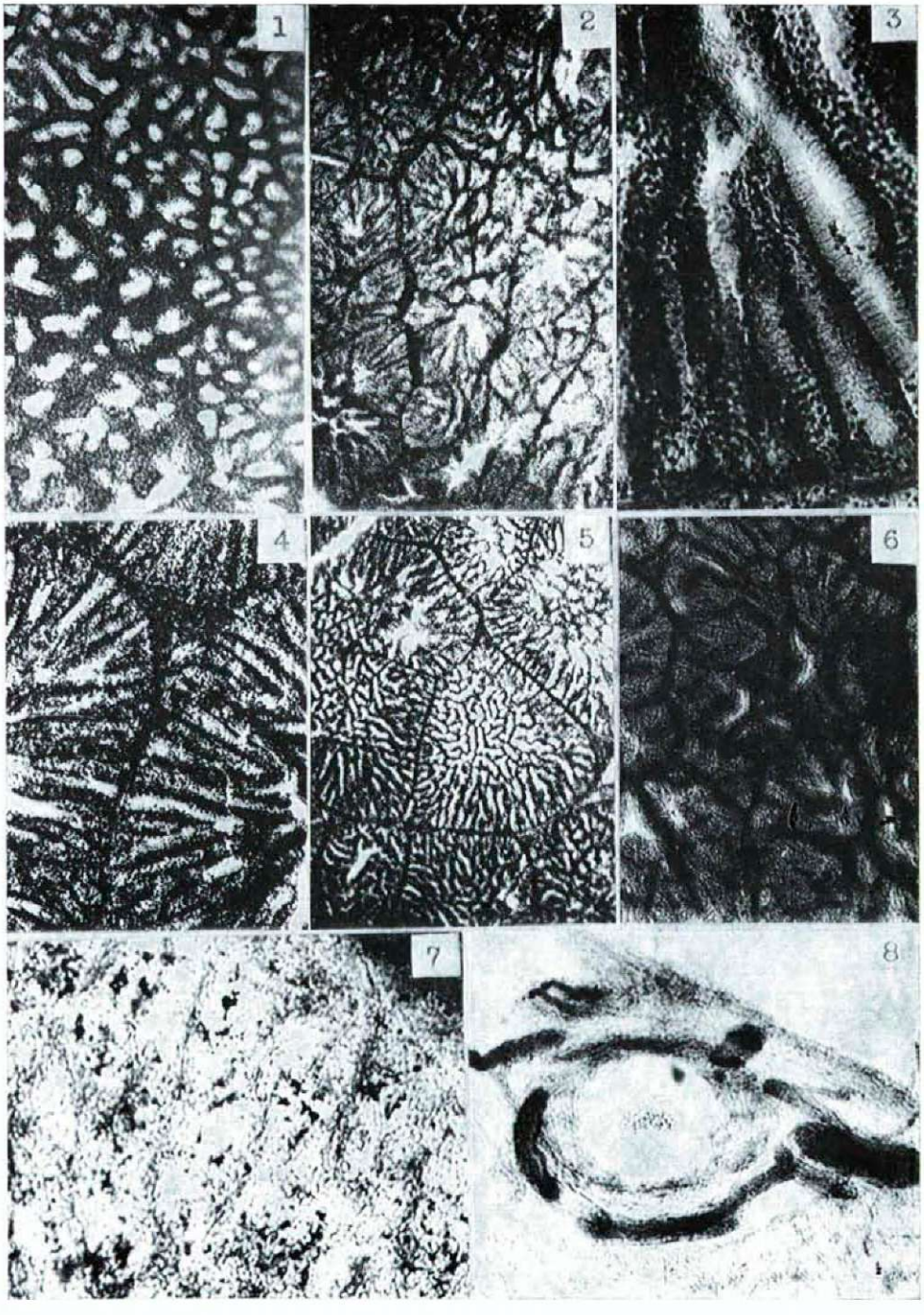
Arterienäste ziehen stets in unmittelbarer Nähe zueinander. Dicke Fasern werden nur an diesen sichtbar, in ausgesprochener Form aber nur an den Hauptästen. Die Selbständigkeit der dicken Fasern ist ebenfalls immer auf das entschiedenste nachweisbar. Terminal erscheinen an den dicken Fasern kleinere oder grössere neurofibrilläre Endlamellen (Abb. 2, g). Die Endlamellen sind einzelstehend und bilden nie verzweigende Systeme. Bei diesen dicken Fasern dürfte es sich auf Grund ihrer Endigungen um sensorische *Trigeminus*-Fasern handeln, die als Pressorezeptoren der grösseren Arterien und Ausführkanälchenwand fungieren.

Unterschiede

Die Harderschen Drüsen der verschiedenen Vogelarten weisen sowohl hinsichtlich ihrer Grösse, Gestalt und Struktur, als auch betreffs ihres Sekretes Unterschiede auf. Die am längsten bekannte und wesentlichste Abweichung ist, dass die Drüsen der Wasservögel besonders gross sind und fettartige Substanz enthalten (12). Wir begegnen aber nicht nur diesem Unterschiede. Auch die seröse Hardersche Drüse der übrigen Vögel weist histologisch — von der zusammengesetzten, beerenförmigen Form der Hausvögel bis zu der speziell zusammengesetzten, röhrenförmig strukturierten Form bei den Raubvögeln — die verschiedensten Abweichungen auf, was überzeugend aus der bei gleicher Vergrösserung hergestellten Aufnahmenserie (Tafel I, 1—6) hervorgeht. Besondere Beachtung verdienen die Bilder (3—4), die aus der Drüse von Raubvögeln hergestellt wurden und deutlich erkennen lassen, dass sie histologisch eher Nieren- als Speicheldrüsenstruktur aufweisen. Diesen Abweichungen entsprechend wäre mit Recht zu erwarten, dass auch die Nervenversorgung unterschiedliche quantitative und qualitative Verhältnisse aufweise. Dies ist jedoch nicht der Fall. Hinsichtlich der Innervation stimmen die Harderschen Drüsen nahezu überein. Grösse und Zahl der Ganglien, Zahl und Beschaffenheit der die Drüsensubstanz versorgenden Nervenfasern sind vollkommen gleich zu nennen, woraus sich ergibt, dass bei Vögeln mit grosser Harderscher Drüse die Schnitte weitaus seltener Ganglien aufweisen und auch die Innervation in der Umgebung der Kammern relativ ärmer ist als bei den Vögeln mit kleiner Harderscher Drüse. Jeder der 6—8 aus der Drüse von Vögeln, die über eine kleine Hardersche Drüse verfügen (z. B. *Columba*), herstellbaren Schnitte enthält einen kleinen Ganglienanteil und in jedem Schnitt wird das die verzeigenden Arterien verfolgende, reiche Nervengeflecht sichtbar. Der relativ kleinere Umfang erklärt auch die reiche Nervenversorgung der Harderschen Drüse der Raubvögel, und das verhältnismässig grössere Ausmass die ärmlichere Innervation im Falle der Singvögel. Die Pigmentiertheit des zwischen den Drüsenkammern befindlichen Gewebes ist nur für Raubvögel typisch. Die pigmenthaltigen Zellen sind klein, eckig und verzweigen nie (Tafel I, Abb. 7).

Tafel

1. *Columba domestica:* Struktur der Harderschen Drüse
2. *Meleagris gallopavo:* „ „ „ „
3. *Buteo lagopus:* „ „ „ „
4. *Circus pygargus:* „ „ „ „
5. *Larus ridibundus:* „ „ „ „
6. *Turdus merula:* „ „ „ „
7. *Falco cherrug:* Pigmentzellen
8. Columba *domestica:* Cholinesteraseaktivität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Die Frage der Doppelinnervation

Die physiologischen Versuche haben die doppelte Innervation der Drüsen erwiesen (3), und auf Grund dessen wird die Innervation der Speicheldrüsen in den meisten physiologischen Handbüchern als zweifacher Natur: sympathischer und parasympathischer, betrachtet. Die Morphologie vermag jedoch in den meisten Fällen diese zweierlei Systemen entstammenden Nervenfasern weder makroskopisch, noch an Hand mikroskophischer Untersuchungen zu bekräftigen und behauptet eher den sympathischen oder den parasympathischen Charakter der einzelnen Speicheldrüsen (11). Auf Grund unserer an der Harderschen Drüse durchgeführten Untersuchungen sprechen auch wir uns für den letzteren Standpunkt aus. Die Innervation der Harderschen Drüse erweist sich in makroskopischen und mikroskopischen Untersuchungen gleichermassen als von sympathischen Charakter. Eine weitere Bekräftigung hierfür lieferten die mit der Gerebtzoffschen Cholinesterasemethode angestellten Untersuchungen, die folgendes feststellen liessen. In den Ganglien ist die spezifische Cholinesteraseaktivität keine grosse, die Ganglienzellen wiesen hinsichtlich der Intensität der Reaktion keine wesentlichen Unterschiede auf. Jene Stämme, die die Ganglien verlassen hatten, besassen überhaupt keine Cholinesteraseaktivität. Die intensivste Aktivität trat an einzelnen Fasern des Geflechtes der eintretenden Blutgefässe in Erscheinung (Tafel I, Abb. 8.). In den Nervengeflechten der kleineren Blutgefässe dagegen traten derartige Fasern schon nicht hervor. Die äusseren Wandschichten der in der Drüse ziehenden grösseren Arterien weisen eine diffuse Aktivität auf, die aber aufhört, sobald sie zu kleineren Arterien werden. In der Umgebung der Endkammern war nirgends eine Aktivität zu verzeichnen. Unter Berücksichtigung der Ergebnisse der einschlägigen Untersuchungen (3), die zu der Feststellung geführt haben, dass cholinesteraseaktiv die parasympathischen und sympathischen präganglionären und die parasympathischen postganglionären, sowie die zentralen sensorischen Fasern sind, und wenn man die an den Ganglienzellen der Harderschen Drüse beobachtete Aktivität mit der hochgradigen Aktivität vergleicht, die sich am Herzen (1) oder an den parasympathischen Zellen des *Ganglion ciliare* bemerkbar macht (10), so kann die obige Behauptung als erwiesen gelten, wonach die Ganglienzellen der Harderschen Drüse sympathischen Charakters sind und in den die Endkammern umgebenden Geflechten nur die adrenergen sympathischen, postganglionären Fasern endigen. Die an einzelnen Nervenfasern der eintretenden Arterien zutagetretende Aktivität weisen unseres Erachtens die dicken, sensiblen Trigeminusfasern auf.

Zusammenfassung

Anlässlich der Untersuchung der Innervation der Harderschen Drüse von Vögeln verschiedener Lebensweise konnte folgendes festgestellt werden:

Makroskopisch sichtbare Nervenverbindungen liegen nicht vor.

Die mikroskopisch nachweisbare reiche Innervation stammt von den Fortsätzen der in der Bindegewebskapsel der Drüse Platz nehmenden Ganglien und den Nervengeflechten der Blutgefässe.

Die Zellen der Ganglien sind multipolarisch, vom Typ DOGIEL II, die aus ihren postganglionären Fasern sich zusammentuenden Nervenstämme dringen — den Verzweigungen der Arterien folgend — in die Drüsensubstanz ein.

Die Geflechte der Blutgefässe bestehen aus dünnen sympathischen und dicken sensiblen Fasern. Die dünnen Fasern umgeben die Endkammern, während die dicken die sensiblen Elemente der Gefässe und der Ausführkanälchen sind.

Die um die Endkammern angeordneten terminalen Geflechte stellen die Endverbindung zwischen den Drüsenzellen und dem Nervensystem dar. Die terminalen Fasern dringen auch zwischen die Drüsenzellen vor, ohne jedoch in das Plasma einzutreten.

Gestalt, Grösse und histologische Struktur der Drüse sind je nach den Vogelarten verschieden, verursachen aber in der Innervation keine wesentlichen Unterschiede. Menge und Beschaffenheit der in ihr vorhandenen Ganglien und Fasern stimmen bei den verschiedenen Vögeln vollkommen überein. Diese quantitative Übereinstimmung ergibt sich aus der relativ ärmlicheren Innervation der aus grösseren Endstücken aufgebauten, umfangreicheren Drüsen und der verhältnismässig reicheren Innervation der kleineren Drüsen.

Die doppelte Innervation der Drüse ist morphologisch nicht zu beweisen. — Auf Grund der Nervenverbindungen und der Cholinesteraseaktivität kann die Hardersche Drüse als ein sympathisch innerviertes Organ gelten.

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DIE WIRKUNG DER ANAEROBIOSE AUF DIE DIAPAUSE-PUPPEN DES AMERIKANISCHEN WEISSEN BÄRENSPINNERS (HYPHANTRIA CUNEA DRURY)

von

L. VARJAS

Institut für allgemeine Zoologie und Biologie der József Attila-Universität Szeged, Ungarn
(Dir.: Prof. Dr. A. ÁBRAHÁM)

In der Natur müssen sich gewisse Insektenarten, bzw. bestimmte Entwicklungsformen derselben zuweilen mehr oder weniger lange Zeit in sauerstoffarmer oder sauerstofffreier Umgebung aufrecht erhalten. Dies ist nicht nur bei den Endoparasiten, sondern auch im Falle der frei lebenden Organismen keine Seltenheit. Den in stagnierenden Stillwasserregionen oder in irgendwelchem in Zersetzung begriffenen organischen Material (Leichen, Kompost, Dünger) sich aufhaltenden Insekten steht gewöhnlich wenig Sauerstoff zur Verfügung, und ähnlich verhält es sich in wenig gelüfteten, an organischen Stoffen reichen (Sumpf- und Moor-) Böden. Anhaltende oder vorübergehende Überschwemmungen, Regenfälle, Schneeschmelze oder Grundwasseranstiege können den Sauerstoffnachschub für die im Boden lebenden Insekten wesentlich behindern. Auch in praktischer Hinsicht, z. B. vom Gesichtspunkte des Pflanzenschutzes, ist es nicht uninteressant zu wissen, wie lange gewisse Insekten maximal ohne Sauerstoff zu leben vermögen und welchen Einfluss die Anaerobiose auf ihren Organismus, ihre weiteren Lebensfunktionen usw. hat.

Die Möglichkeit, Dauer und Auswirkungen der Anaerobiose werden vor allem von den in Ermangelung von Sauerstoff sich abspielenden energieerzeugenden Prozessen bestimmt. In der insekten-physiologischen Literatur wurde die Möglichkeit spezieller anaerober fermentativer Reaktionen (z. B. Fettsäure $\rightarrow CO_2+H_2$) oder Umbauprozesse (z. B. Glykogen $\rightarrow$ Fett) erwogen, doch wird im allgemeinen als anaerobe Energiequelle auch im Bereich der Insekten die aus den Geweben der Wirbeltiere wohl bekannte Milchsäure-Glykolyse akzeptiert. Dies geht z. B. deutlich aus den Arbeiten von SLATER (1928) und BRAND (1951) hervor. Auf Grund dieser sogenannten Milchsäure-Theorie hat man die physiologisch-biochemischen Erscheinungen der Insekten-Anaerobiose zu erklären versucht, doch haben sich gerade in dieser Beziehung auch zahlreiche Schwierigkeiten ergeben. Nach GILMOUR (1940) betrug z. B. die Tilgung der „O_2-Schuld" bei *Zootermopsis*-Imagos nur 50%, und AGRELL (1953) fand bei *Calliphora*-Puppen nach der Anaerobiose keine Atmungserhöhung. Die gebildete Milchsäure stand gewöhnlich nicht im Verhältnis zu der verbrauchten Glykogenmenge, bzw. zu der Dauer der Anaerobiose. Dies ging u. a. aus den Untersuchungen von BLANCHARD und DINULESCU (1932) an *Gastrophilus*-Larven, von DAWIS und SLATER (1928) an *Periplaneta*-Imagos und von GILMOUR (1941) an *Tenebrio*-Larven hervor. BARRON und TAHMISIAN (1948), sowie HUMPHREY und SIGGINS (1949) beobachteten bei anaerob gehaltenen *Periplaneta*- bzw. *Locusta*-Muskeln eine besonders spärliche Milchsäureproduktion.

Im letzten Jahrzehnt hat sich das Bild einer besonderen Insekten-Glykolyse entwickelt, über die wir einen Begriff aus den Mitteilungen von CHEFURKA (1959) bzw. ZEBE und MC SHAN (1957) oder aus dem Buche von GILMOUR (1961) erhalten. Es hat sich nämlich herausgestellt, dass in den Insektengeweben, in erster Linie in den Muskeln, die α-Glycerophosphat-Dehydro-

genase (GDH)-Aktivität die Aktivität der Milchsäure-Dehydrogenase (LH) gewöhnlich weit übersteigt, und so das Endprodukt der Glykolyse in erster Linie α-Glycerophosphat und Brenztraubensäure ist. Besonders interessant ist die Bildung des α-Glycerophosphats, weil diese Verbindung in der Energielieferung der Insektenmuskeln eine erstklassige Rolle spielt und gleichzeitig nach den meisten Forschern auch die Quelle für das in den einzelnen Diapause-Insekten zur Anreicherung gelangenden Glycerins ist, welches — wie auch SALT (1961) konstatierte — die winterliche Frostbeständigkeit der Tiere erhöht. Wir haben allen Grund, die bisherigen Ansichten bzgl. der Anaerobiose der Insekten einer Revision zu unterziehen, da diese sich ja vorwiegend um die schon überholte Milchsäure-Theorie gruppierten.

Ich stecke mir vor allem das Ziel, bei einer Diapause-Puppe, die im wesentlich nur den Grundstoffwechsel zeigt, zu ermitteln, wie sich die Frage der mit der Anaerobiose zusammenhängenden „O_2-Schuld" gestaltet. Daneben waren gewisse Daten hinsichtlich der maximalen Dauer der Anaerobiose, sowie über den Einfluss des O_2-Entzuges auf das Puppenstadium und den Habitus des ausschlüpfenden Imago zu gewinnen.

Material und Methoden

Das Material zu den vorliegenden Versuchen waren Diapause-Puppen des amerikanischen weissen Bärenspinners (*Hyphantria cunea* DRURY). Die in den Herbstmonaten (September—Oktober) gesammelten alten Raupen der II. Generation wurden im Freien aufgezogen. Als Nährpflanzen diente Weiden (*Salix*-Arten). Die Raupen begannen sich zu Ende Oktober, bzw. Anfang November einzupuppen. Die Puppen überwinterten im Freien, worauf ich sie dann einmal im Anfang April des nächsten Jahres und ein andermal Ende Januar ins Laboratorium brachte. Die hier aus ihrem Gespinst befreiten Puppen kamen — auf Watte gebettet — in Petri-Schalen. Im ersteren Falle wurden die Tiere bei Raumtemperatur (etwa 20° C) gehalten und einer kurzfristigeren Anaerobiose unterworfen. Die Ende Januar eingetragenen Individuen kamen in ein Thermostat von 25° C und wurden später zum Studium der länger dauernden Anaerobiose verwendet. Sämtliche Versuche wurden relativ kurze Zeit (2—5 Tage) nach der Einbringung der Puppen in das Laboratorium in Angriff genommen, so dass die Tiere noch in der letzten, milde Wärme beanspruchenden Diapausen-Phase untersucht werden konnten. Auch die Werte des Sauerstoffverbrauchs verraten, dass in dieser Phase die im Anschluss an die Diapause eintretende Morphogenese noch keineswegs eingesetzt hatte. Den nicht verwendeten (und teilweise den benutzten) Puppen begannen die Schmetterlinge erst nach 2—3 Wochen zu entschlüpfen. Die untersuchten Puppen waren 9—12 mm lang, 3—4 mm breit und 80—150 mg schwer. Sie wurden für kürzere — 0,5; 1; 1,5; 2; 3 und 24 Stunden —, bzw. längere Zeit — 2; 3, bzw. 6 Tage — in kleine, gut verschlossenen Röhrchen in mit alkalischem Pyrogallol gewaschenes, mit erhitztem $CaCl_2$ getrocknetes Stickstoffgas gegeben, wobei — nach Geschlechtern geteilt — Gruppen von 6—8—10 Puppen verwendet wurden.

Der Sauerstoffverbrauch der Tiere wurde bei 25° C im Warburg-Apparat in Luft-Atmosphäre und ohne Schütteln gemessen. Die Messung des O_2-Verbrauchs unmittelbar vor der Anaerobiose dauerte fallweise 40, bzw. 90 Minuten und nachher 15, 25, bzw. 90 Minuten. Diese zweite Messung darf — entsprechend der Methode — erst mit einer gewissen Verspätung (10—40 Minuten) nach der Anaerobiose vorgenommen werden. Der Sauerstoffverbrauch wurde in μl/h/100 mg Lebendgewicht ausgedrückt angegeben.

Ergebnisse

In Tabelle 1 und 2 sind die Ergebnisse je einer Versuchsserie angeführt. Es fällt auf den ersten Blick auf, dass der Sauerstoffverbauch der Puppen weder nach der kürzeren, noch nach der längeren Anaerobiose wesentlich verändert war. Nach der langfristigeren Anaerobiose war eher eine gewisse abnehmende Tendenz festzustellen. Den Ergebnissen ist somit zu entnehmen, dass im Laufe der Anaerobiose der Diapause-Puppen der *Hyphantria cunea* (zumindest in der fraglichen Periode der Diapause) eine „O_2-Schuld" nicht zustande kommt, d. h. bei diesen Tieren die postanaerobe Atmungssteigerung ausbleibt. Es ist höchst unwahrscheinlich, dass die eventuelle Atmungserhöhung in jedem einzelnen Falle vollkommen ausserhalb der Beobachtungszeit eingetreten wäre und deshalb in Tabellen jegliche Spur davon fehlt.

Interessant ist, dass bei einigen nicht im Diapause-Zustand befindlichen Puppen ähnliche Ergebnisse erhalten worden sind. Die Untersuchungen von AGRELL (1953) wurden bereits erwähnt. Meines Erachtens kam es bei den von GAARDER (1918) an *Tenebrio*-Puppen durchgeführten Versuchen ebenfalls nicht zur Tilgung der „O_2-Schuld", obwohl der Autor sich auf eine gewisse, verspätet erscheinende Atmungserhöhung beruft. Seine Tabellen entbehren der Beweiskraft.

Auf der Suche nach einer Erklärung für die gemachten Beobachtungen halte ich die Möglichkeit speizeller anaerober energieliefernder Reaktionen nicht für wahrscheinlich. Wenn ein solcher Mechanismus bestünde, so würde möglicherweise auch der normale aerobe Stoffwechsel gewisse Besonderheiten verraten. Meine an weiblichen Puppen zu dieser Periode vorgenommenen RQ-Bestimmungen ergaben Werte von rund 0,77, woraus derartige Schlüsse nicht gezogen werden können. Das Ausbleiben der Abtragung der „O_2-Schuld" lässt sich auf Grund der speziellen Insekten-Glykolyse gut erklären.

Die terminale Energiequelle ist aller Wahrscheinlichkeit nach Kohlehydrat (Glykogen, Trehalose, Glukose), und das Endprodukt der anaeroben Glykolyse neben den geringen Mengen Milchsäure α-Glycerophosphat und Brenztraubensäure. Nach WYATT und MEYER (1959) bleibt die α-Glycerophosphat-Dehydrogenaseaktivität auch während der Diapause erhalten. Aus der Tatsache, dass die Brenztraubensäure stets in relativ kleineren Mengen nachweisbar ist — mit welcher Frage sich CHEFURKA (1959) und KUBIŠTA (1958) auch besonders beschäftigen, — ist darauf zu schliessen, dass diese Verbindung und die noch geringeren Mengen Milchsäure wahrscheinlich von dem Puffer-Mechanismus der Gewebe gebunden wird. Das Schicksal des α-Glycerophosphats ist — wie zur Zeit der Diapause auch unter aeroben Umständen —, dass es hydrolysiert und Glycerin liefert. Dies beweisen übrigens auch die Untersuchungen von WILHELM (1960), wonach bei Diapause-Puppen die Anaerobiose die Glycerinanreicherung steigert. Das Glycerin ist unmittelbar nicht oxydierbar. Aus den Versuchen von CHINO (1957) wissen wir, dass es auch zur Glykogen-Resynthese erst zu Ende der Diapause verbraucht wird. Möglicherweise stellt bei den Insekten in der Frage der „O_2-Schuld" das α-Glycerophosphatbildungsverhältnis und der Grad der Hydrolyse den entscheidenden Faktor dar, und die in der Literatur angegebenen verschiedenen Befunde dürften hiermit zu erklären sein. Wenn im Laufe der Anaerobiose in überwiegender Menge diese Verbindung

gebildet wird und sich in Glycerin weiterverwandelt, so kann die Tilgung der „O_2-Schuld" ausbleiben.

Dreitägige Anaerobiose wurde von den *Hyphantria*-Puppen ohne jede wahrnehmbare Schädigung vertragen. Die beiliegende Abbildung zeigt ebenfalls, dass die aus solchen Puppen hervorgegangenen Schmetterlinge keinerlei Anomalien verraten. Sechstägiger Sauerstoffentzug dagegen ist bereits von vernichtender Wirkung: hier schlüpfte schon kein einziger Falter aus. Hieraus wird wahrscheinlich, dass bei der fraglichen Art zu der gegebenen Periode der Diapause die maximale Dauer der Anaerobiose etwa 4—5 Tage beträgt. Ein Vergleich dieser Befunde mit der Tabelle von BRAND (1951) lässt feststellen, dass die Diapause-Puppen von *Hyphantria cunea* den Sauerstoffmangel relativ lange Zeit zu überleben vermögen. In Verbindung hiermit ist ein Hinweis auf die Feststellung von HARVEY (1962) lohnenswert: "... the diapausing eggs are resistant to anaerobiosis" (Seite 70), die eventuell bis zu einem gewissen Grade auch für die Diapause-Puppen Gültigkeit besitzt.

Die Anaerobiose beeinflusste die Dauer des Puppenstadiums in dieser Periode der Puppenentwicklung und Diapause bei beiden Geschlechtern nicht in der gleichen Weise. Da meine diesbezüglichen Untersuchungen weniger eingehende waren, war lediglich in Erfahrung zu bringen, dass der 2—3-tätige Sauerstoffmangel bei den weiblichen Tieren das Puppenstadium um eine längere Zeitspanne als die Anaerobiose, und die 3-tägige Anaerobiose bei Männchen kürzere Zeit als drei Tagen verlängerte. Bei den männlichen Tieren war überraschenderweise die 2-tägige Anaerobiose eher von entwicklungsverkürzendem Effekt. Die gesteigerte Empfindlichkeit der weiblichen Exemplare dürfte mit ihrem regeren Stickstoff-Stoffwechsel im Zusammenhang stehen, denn nach Befunden von JASIČ und MACKO (1961) verfügen die weiblichen *Hyphantria*-Puppen über einen höheren Stickstoffgehalt. In Verbindung mit der bei männlichen Exemplaren beobachteten stimulierenden Wirkung verdient die Ansicht von LEES (1961) Beachtung, wonach während der sogenannten Diapausen-Entwicklung: "... the final high temperature phase is favoured by anoxia" (Seite 137). Diesen günstigen Einfluss dürften bei den weiblichen Puppen, bzw. im Falle längerer Anaerobiose — gewisse endogene Faktoren beeinträchtigt haben.

Zusammenfassung

Hyphantria cunea-Puppen wurden in der letzten, wärmebeanspruchenden Phase der Diapause für 0,5; 1; 1,5; 2; 3 und 24 Stunden, bzw. für 2; 3 und 6 Tage in ein anoxibiotisches Milieu (N_2-Atmosphäre) gebracht und dabei folgendes beobachtet:

1. Die maximale Anaerobiose-Dauer beträgt etwa 4—5 Tage.

2. Nach den verschieden langen Anaerobiosezeiten war in keinem einzigen Falle eine vorübergehende Steigerung des Sauerstoffverbrauches festzustellen.

3. Die 3-tägige Anaerobiose bewirkte gewöhnlich eine Verlängerung der Entwicklungsdauer der Puppen, doch erwiesen sich in dieser Beziehung die weiblichen Exemplare als empfindlicher. Bei den männlichen Puppen war die 2-tägige Anaerobiose von ausgesprochen entwicklungsstimulierendem Einfluss.

4. Aus den nach der 3-tägigen Anaerobiosen am Leben gebliebenen Puppen schlüpften habituell normale Imagos aus.

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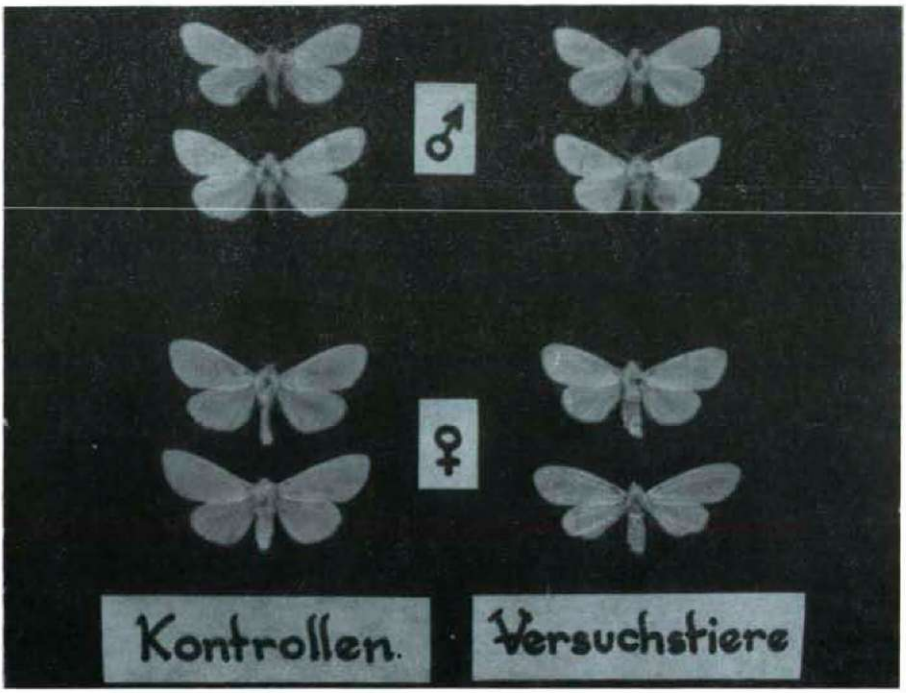

Die Imagos von *Hyphantria cunea* DRURY., die aus solchen Puppen hervorgegangen sind, welche während der letzten Phase der Diapause eine dreitägige Anaerobiose überlebt hatten.

Tabelle 1

Die Wirkung kurzfristiger Anaerobiose auf den O_2-Verbrauch der Diapause-Puppen von *Hyphantria cunea* DRURY.

Dauer der Anaerobiose Stunden	Geschlecht	O_2-Verbrauch µl/h/100 mg Lebendgewicht			
		Kontrollen		Versuchstiere	
		vor d. Anaer.	nach d. Anaer.	vor d. Anaer.	nach d. Anaer.
0,5	♀	12,3	16,1	14,1	14,3
1	♀	—	—	14,5	9,8
1,5	♀	12,3	12,9	14,6	11,5
2	♀	14,9	17,5	12,8	14,0
3	♀	16,5	18,5	14,5	11,7
24	♂	19,4	20,8	20,1	17,0

Tabelle 2

Die Wirkung langfristiger Anaerobiose auf den O_2-Verbrauch der Diapause-Puppen von *Hyphantria cunea* DRURY.

Dauer der Anaerobiose Tage	O_2-Verbrauch µl/h/100 mg Lebendgewicht							
	♂				♀			
	Kontrollen		Versuchstiere		Kontrollen		Versuchstiere	
	vor d. Anaer.	nach d. Anaer.	vor d. Anaer.	nach d. Anaer.	vor d. Anaer.	nach d. Anaer.	vor d. Anaer.	nach d. Anaer
2	9,7	10,8	14,3	14,1	11,4	11,9	12,1	12,0
3	11,2	12,3	10,5	9,6	15,6	14,5	10,7	7,5

CIRRIPEDIA-PEDUNCULATA-RESTEN AUS DEM SÜMEGER SENON

von

L. Czabalay-Benkő und G. Kolosváry

Staatliches Geologisches Anstalt in Budapest Ungarn. und Systematisch - Zoologisches Institut der Universität Szeged, Ungarn

Bei der Sortierung des Mikromollusken-Materials der Sümeger Senon-Gebilde kamen einige stielhaltige Cirripeden-Skelettelemente zum Vorschein. Ihre Bedeutung — abgesehen davon, dass es sich um interessante Funde handelt — besteht darin, dass sowohl in der ungarischen, als auch in der ausländischen Literatur nur wenig Angaben über mesozoisches Material vorliegen. Die meisten Forscher befassen sich mit Terziär- oder rezenten Funden. — L. Bertrand, (1891), Cheetnam (1963), P. P. C. Hoek (1907), H. A. Pilsbry (1907), Seguenza (1876), T. H. Withers (1936—1953) und der ungarische Szörényi (1934) beschreiben Eozän-Residuen. Das Material aus dem Mesozoikum ist eingehend von C. Darwin (1851) und Withers (1828— Trias-Jura und 1935 Kreide) behandelt worden. Ausgezeichnete Zusammenfassungen liegen noch von Krüger (1940) als Übersicht über das rezente und fossile Material vor.

Die korallen-molluskenhaltige Mergellehm-Gruppe des Kampaniens lässt sich faunistisch in zwei Stufen gliedern. Innerhalb dieser hat die stratigraphische Synthese die Feststellung zahlreicher Biofacies ermöglicht: *1.* Schneken — *Pecten* — *Cardium* — Korallen-Niveau und *2.* Muschel — *(Nucula* — *Corbula)* Korallen-Niveau, welch ersteres in zwei weitere Biofacies zerlegbar ist: glaukonische und Pirenellen-Facies.

Die glaukonische Biofacies enthält vorwiegend Glaukonien mit vereinzelten Corbulen und Cyrenen, welche Faunen-Assoziation ein Beweis für Meereswasser mit vermindertem Salzgehalt darstellt. Die an den Glaukonien gefundenen Spuren des Bohrschwammes *Cliona vastifica* Volz stehen nicht im Widerspruch zu der obigen Feststellung. Diese eurytherme, kosmopolitische Art, die auch heute — zusammen mit *Cliona celata* — in der Adria lebt, ist ein charakteristisches Mitglied der litoralen Zone. In dem 2—10 m tiefen Abschnitt ist sie häufig, in der 10—40 m tiefen Vertikalzone aber massenhaft anzutreffen.

Die Fauna der Pirenellen-Biofacies hat schon eher Salzwasser-Charakter, sie ist reich an Korallen, Bryozoen und Mollusken.

Typische Schnecken sind: *Pirenella münsteri* (Keferstein), *Pirenella hoeninghausi* (Keferstein), *Desmieria goldfussi* (Zekeli), *Pseudamaura bulbiformis* (Sowerby), *Aptyxiella gracilis* (Münster) und *Aptyxiella flexuosa* (Sowerby). In der grössten Individuenzahl ist *Turritella tricincta* (non Münster) vertreten. In diesen Faunenbiocönose kamen auch die stieltragenden Cirripedien-Reste zum Vorschein.

Es muss erwähnt werden, dass wir sowohl die im Glaukonen-Niveau beobachteten. *Cliona vastifica* VOLZ-Spuren, als auch die im Pirenellen-Niveau gefundenen Reste von stielhaltigen Cirripeden nur dort gewahr wurden, wo diese Formationsgruppe sich unmittelbar dem hippurithaltigen Kalkstein anschliesst. Sie war also in diesem Falle die für die felsenbewohnende Facies charakteristische Sand-Facies des ufernahen Meeresteiles, wo die Bewegung des Meereswassers eine sehr intensive gewesen sein dürfte. Die biotopartige Anordnung der Fauna ist anzunehmen, beweisen doch unsere Sammelergebnisse auch, dass an einzelnen Flecken auch massenhaft Cycloliten anzutreffen waren.

Über die vertikale Verbreitung der stieltragenden Cirripeden liegen nur wenig Angaben vor. CHEETHAM (1936) stellt fest, dass die heute lebenden *Scalpellum*-Arten vorwiegend den tiefen Meereszonen angehören. So sind *Scalpellum* bis zu 30—4000 Klafter, *Euscalpellum* bis zu 50—1200 und *Acroscalpellum* bis zu 30—2000 Klafter Tiefe verbreitet. *Mitella (Pollicipes) litoralis* lebt in Europa, Nordamerika, Japan, Neuseeland und China, während der *Lithotrya*-Genus in der Riff-Zone des Pazifiks, an der Küste Floridas und an den Gestaden der grossen Bahama-Bank lebt (PILSBRY, 1907, 1953, und NEWELL, 1959).

Die Arten des Senon sind grossenteils augestorben, so dass auf ihre ehemaligen Lebensumstände schwer zu schliessen ist. In Kenntnis der übrigen Faunenelemente und auf Grund der bekannten ökologischen Daten kann eine felsbewohnende Facies vermutet werden. Ihre vertikale Verbreitung ging nicht über die Ebben-Zone hinaus und auch ihr Auftreten ist nicht massenhaft zu nennen.

Beschreibung der Funde

Maximale Grösse in Höhe und Breite: 6—7 mm. Farbe grau und dunkelgelb, Ornamentik variabel.

Nach KRÜGER (1940) und Carlsson (1942) sind aus dem Senon die folgenden Genera bekannt: *Zeugmatolepas, Calantica (Titanolepas), Cretiscalpellum, Loriculina (Stramentum), Brachylepas, Pycnolepas, Virgiscaplellum, Calantica valida (Steenstrup), Calantica nilssoni (Steenstrup)* und *Brachylepas guascoi (Bosquoet).* — Im Senon und auch heute lebende Genera sind: *Scillaelepas, Acroscalpellum, Neoscalpellum, Calantica* und *Squama.*

Aufzählung der Funde:

a) Eine kompakte *Carina,* 7 mm. Eine typische Querraffung ist wahrnehmbar, jedoch in rudimentärer Form als beim Typ (Tafel I, Abb. 1).

b) Sehr variable *Terga.* Maximale, aber unvollkommene Länge 6 mm. Breite gewöhnlich 3 mm. *Apex* etwas gebogen. An der Oberfläche verlaufen 3—4 Längsrippen. Sie erinnern an *Acroscalpellum*-Plättchen. Die 11 gleich gut erhaltenen Funde machen ihre Zugehörigkeit zu mehreren Individuen wahrscheinlich (Tafel II, Abb. 5 und Tafel III, Abb. 11—13).

c) Mehrere *Carina*-artige Lamellen in zwei Varianten:

1. Mit sekundärer Plattenbildung (*Scalpellum,* Tafel II, Abb. 3 und Tafel III, Abb. 1—4 und 6).

2. Ohne sekundäre Plattenbildung (*Virgiscalpellum,* Tafel II, Abb. 2 und Tafel III, Abb. 7—9).

Nach ihrer Erhaltenheit zu urteilen, dürften diese Lamellen etwa zehn Individuen angehört haben, ihre Länge betrug im allgemeinen 5 mm.

d) Eine infralaterale Platte (Tafel II, Abb. 6), sechs *Scuta* (Tafel III, Abb. 5, 10, 14, 15, 16, 17), eine *Carinolaterale* (Tafel II, Abb. 4) und vierzehn *Rostrolaterale* (Tafel II, Abb. 7 und Tafel III, Abb. 18—22).

Die *Rostrolaterale-* und *Carina*-Platten verraten konservativen, d. h. *Virgiscapellum-Acroscapellum*-Charakter. Die stark variablen (modifiziert-elastischen) tergalen Funde deuten eher nur auf die *Terga* von *Acroscalpellum* hin. Progressive Merkmale zeigen die acroscalpelloiden *Carinae,* sofern wir die sekundäre Lamellenbildung als fortschrittliche Spezialisation betrachten. — Regressive Eigenschaften weist die Carina von *Calantica* auf, die wegen ihrer untersetzten und relativ grossen Ausmasse rudimentäre Querriffelung aufweist. Mehrere rezente *Calantica-Carinae* sind schon glatt.

Wir halten für wahrscheinlich, dass sich unter den Residuen auch Lamellen der *Virgiscalpellum darwinianum* (BOSQUET) befinden. Neben dieser Art dürften noch 2—3 *Acroscalpellum,* sowie eine Ur-*Calantica* vorhanden sein. Was die häufigsten *Acroscalpellum*-Reste anbetrifft, kann jene Menge, deren tergale Rippung ganz neu erscheint, provisorisch als *Acroscalpellum longicostalis* n. sp. betrachtet werden, aber mit dem Vorbehalt, dass neben dieser Art noch 1—2 weitere gelebt haben, deren Überreste aber für eine eingehendere Beschreibung nicht hinreichen und Schlussfolgerungen nicht gestatten.

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Erklärung der Abbildungen

Tafel I.

1: *Calantica-Carina*, seitlich und von der Kante her.
9: Liasz *Aporolepas-Scutum*, 4—5 mm gross, zum Vergleich mit den *Scuta* der Funde von Sümeg.
10: Lamellen-Skizze einer stieltragenden *Cirripedia-Thoracica (Lepadida)*.
n: Stiel, cl: *Carinolaterale*, li: *Latus inferior*, rl: *Rostrolaterale*, c: *Carina*, ls: *Latus superior*, s: *scutum*, t: *tergum*.
11: *Calantica-Carina*-Typ.

Tafel II.

2: Vier *Virgiscalpellum-Carina*, 3 mm.
3: Fünf scalpelloide *Carina* mit sekundärer Plattenbildung.
4: *Pisiscalpelloides Rostrolaterale*, möglicherweise aber auch das von einer *Acroscalpellum* stammende *Carinolaterale*.
5. Sieben acroscalpelloide *Terga*, 6 mm.
6: Aussen- und Innenseite eines virgiscalpelloiden *Infralaterale*.
7: Sieben *Rostrolaterale* vom Typ *Acroscalpellum* bzw. *Scalpellum* in verschidenen Aspekten, 3 mm.
8: Fragliches *Rostrum?*

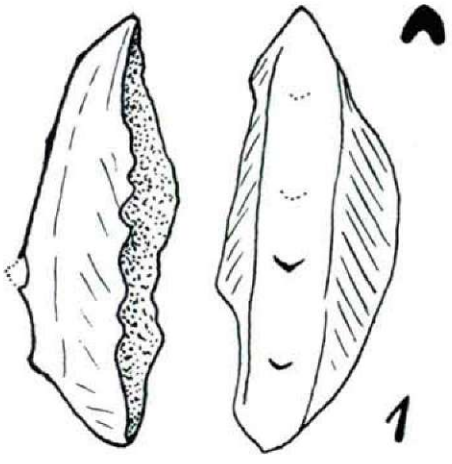
Originalzeichnungen von KOLOSVÁRY.

Tafel III.

1—4: *Carinae* vom Typ *Scalpellum-Acroscalpellum*.
6: *Carina* vom Typ *Scalpellum-Acroscalpellum*.
7—9: *Carinae* vom Typ *Virgiscalpellum*.
5, 10, 14, 15, 16, 17: *Scutum*-Lamellen.
11, 12, 13: *Acroscalpellum*-Terga.
18—22: Rostrolateralien in verschiedenen Aspekten.

Originalaufnahmen von CZABALAY.

I.



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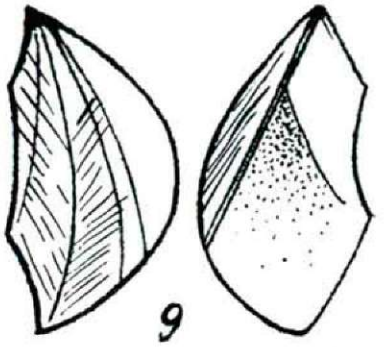

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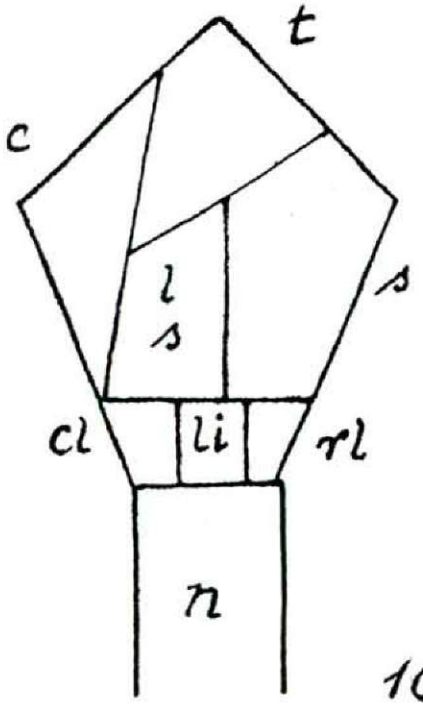

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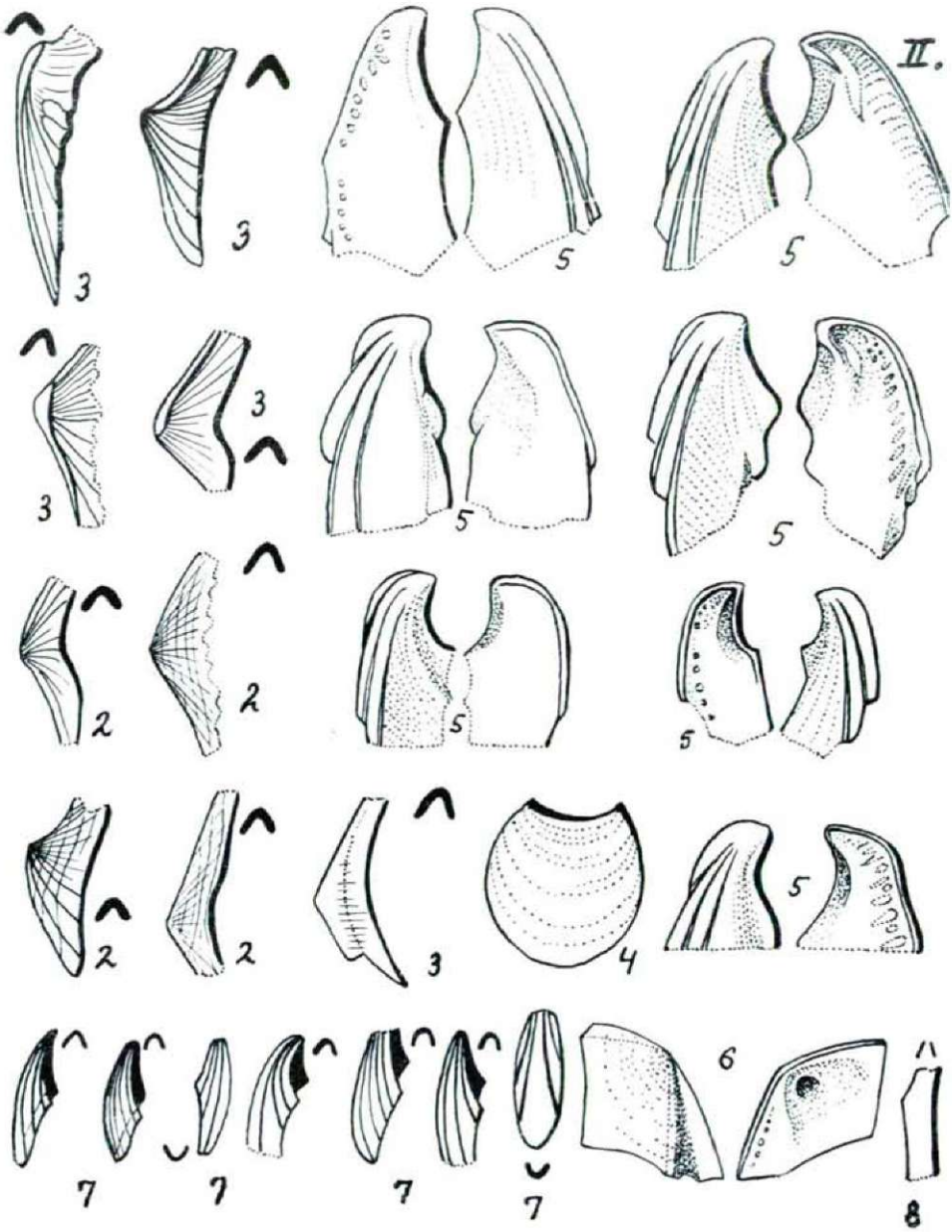
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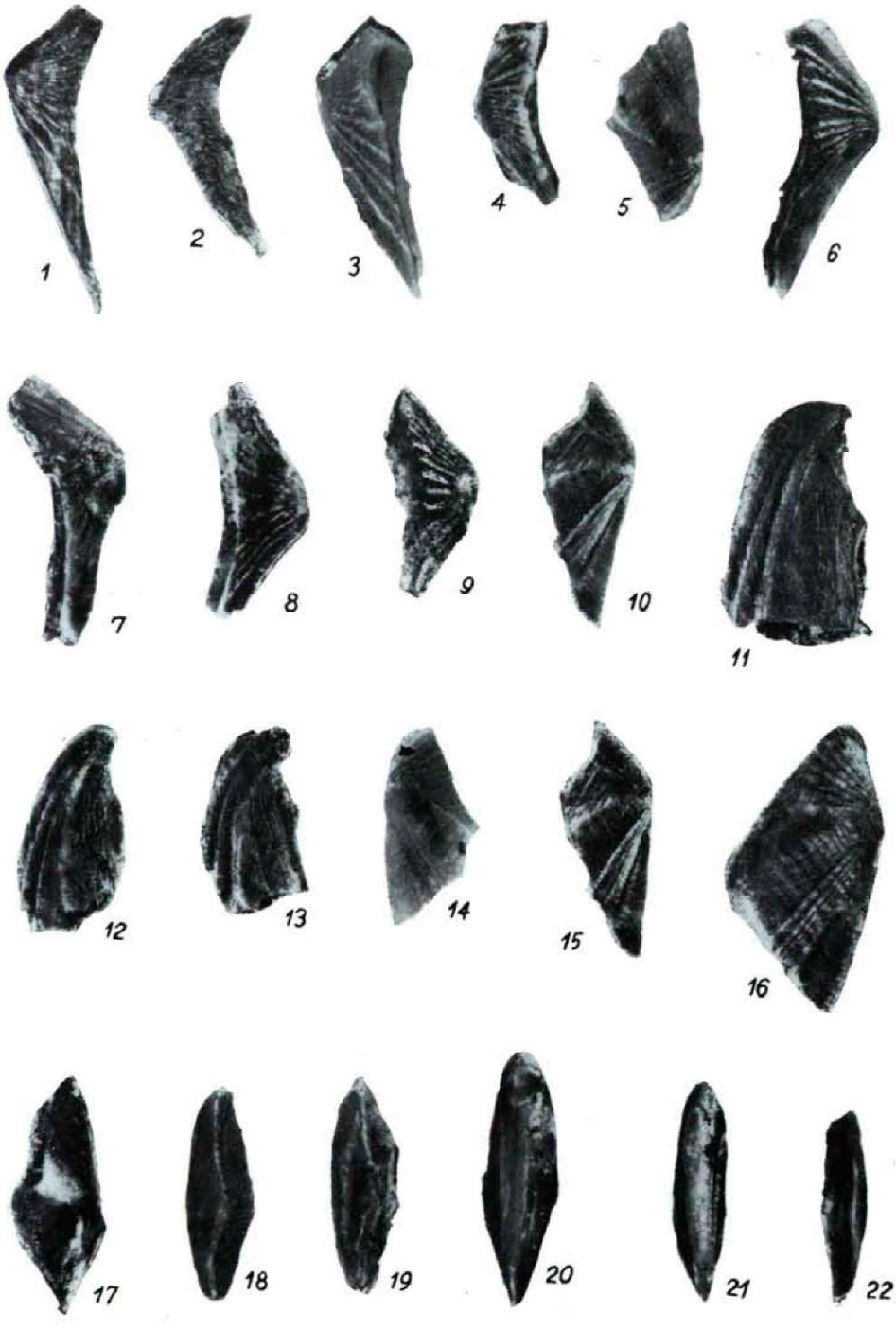
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DAS LEBEN DER TISZA XXIV
LÄNGS-PROFILUNTERSUCHUNGEN DES ZOOPLANKTONS IM ÖSTLICHEN HAUPTKANAL

von

D. GÁL

Systematisch-Zoologisches Institut der Universität Szeged, Ungarn

Seit der Errichtung des Wasserstauwerkes bei Tiszalök hat sich die Fluss-Strecke oberhalb von Tiszalök — auf einer Länge von etwa 50 km — total verändert. Dieser Abschnitt der Tisza weist vom fliessenden Wasser vollkommen verschiedene Eigenschaften auf, und hat sozusagen Stillwasser-Gepräge. Die Geschwindigkeit des Wasserlaufes ist äusserts gering, infolgedessen auch das schwebende Geschiebematerial stark verringert und die Wasserdurchsichtigkeit gross. Entlang des Ufers finden sich die für stehende Gewässer charakterischen Pflanzen — Rohr und Schilf. Von diesem stillwasserartigen Abschnitt der Tisza nimmt der künstlich angelegte Östliche Hauptkanal seinen Ausgang, der in volkswirtschaftlicher Hinsicht von grosser Bedeutung ist (sein Wasser wird zur Berieselung mehrerer tausend Joch Ackerbodens verwendet).

Das Wasser des Östlichen Hauptkanals unterscheidet sich hydrologisch weitgehend von dieser Strecke der Tisza, vor allem in der Geschwindigkeit des Wasserlaufes und den sich hieraus ergebenden Faktoren (Durchsichtigkeit, schwebende Geschiebemassen usw.). Die Geschwindigkeit der Wasserströmung wechselt je nach der Wassermenge, die durch die 5 km von der Mündung gelegene Schleuse bei Tiszavasvári gelassen wird, bzw. je nach der aus dem Kanal zur Bewässerung verwendeten Wassermenge. Zu Bewässerungszeiten ist die Geschwindigkeit des Laufes eine grössere, während in anderen Perioden das Wasser fast stillsteht.

Im Laufe meiner bisherigen Untersuchungen habe ich parallel mit den Sammlungen aus der Tisza nur von einer Stelle des Östlichen Hauptkanals — bei Tetétlen, etwa 80 km von der Mündung entfernt — Sammelproben eingeholt und auch von diesen nur die Rhizopoden aufgearbeitet (7). Die dabei erhaltenen Ergebnisse lieferten kein vollständiges Bild über die Unterschiede zwischen Tisza und Östlichem Hauptkanal, weshalb ich meine Studien auch auf die Rotatorien und Crustaceen ausdehnte, um in Erfahrung zu bringen, welche Veränderungen sich in der Zusammensetzung des Zooplanktons in dem aus der Tisza abzweigenden Östlichen Hauptkanal ergeben.

Am 24. Juli 1963. hatte ich die erste 40 km lange Strecke des Kanals eingehend untersucht, als der Durchfluss ziemlich gross war — 50 m^3/sec — und deshalb das Wasser des Östlichen Hauptkanals wesentlich mehr schwebende Teilchen führte als das Wasser der Tisza oberhalb des Stauwerkes.

Untersuchungsmethoden

Zu den Sammlungen benutzte ich ein Planktonnetz Nr. 25, durch das jedesmal 100 Liter Wasser filtriert wurden, um auch die quantitativen Veränderungen analysieren zu können. Das gesammelte Material wurde an Ort und Stelle mit Formalin konserviert, bei der Aufarbeitung die Proben auf 10 ml

ergänzt, davon festgesetzte Mengen untersucht und die erhaltenen Ergebnisse auf 100 Liter umgerechnet. Proben entnahm ich aus der Tisza an der Mündung des Östlichen Hauptkanals, sowie aus dem Östlichen Hauptkanal auf der ersten 40 km langen Strecke alle 5 km. Die Wassertemperatur betrug 25—25,7° C, die pH-Werte wechselten zwischen 7,1—7,3 (wesentliche Abweichungen zwischen den beiden Gewässern bestanden nicht).

Ergebnisse

Die erhaltenen Ergebnisse sind in Tabelle 1 zusammengefasst, wo die an den einzelnen Sammelstellen gefundenen Individuen auf 100 L berechnet und das prozentuelle Vorkommen der einzelnen Arten angegeben sind.

Jene Ergebnisse, welche die Unterschiede zwischen Tisza und Östl. Hauptkanal widerspiegeln, sind graphisch dargestellt. (An der Waagerechten ist die von der Mündung gemessene Entfernung, und an der Senkrechten die in 100 L Wasser gefundene Individuenzahl eingetragen. O = Tisza an der Mündung des Östlichen Hauptkanals.)

Abbildung 1 veranschaulicht die Veränderungen der Gesamtindividuenzahl, sowie Veränderungen der Individuenzahl der Protozoen, Rotatorien und Crustaceen gesondert. Auffallend ist, dass die Gesamtindividuenzahl an der ersten Strecke des Östlichen Hauptkanals im Verhältnis zur Tisza schon während der ersten 5 km stark, und an der 10 km-Grenze noch weiter abnimmt. (In der Tisza beträgt die Gesamtindividuenzahl 9,000, und 10 km weiter

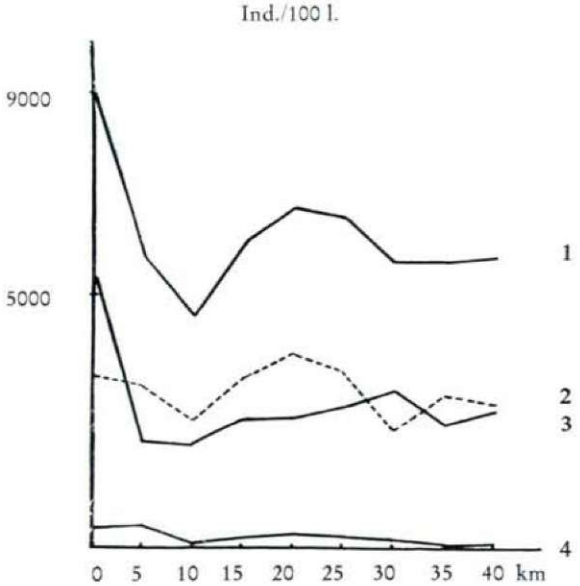

Abb. 1. 1. Gesamtindividuenzahl,
2. Crustacea,
3. Rotatoria,
4. Protozoa.

nur mehr etwa die Hälfte: 4,600/100 Liter.), von hier ab bis zum 20. km erfolgt ein mässiger Anstieg, um dann wieder abzunehmen; nach 30, 35 und 40 km stimmen die Gesamtindividuenzahlen schon fast vollkommen überein.

Die am ersten Abschnitt eingetretene hochgradige Verminderung der Individuenzahl ist vor allem durch die Verringerung der Individuenzahl der Rotatorienarten bedingt. Innerhalb der Rotatorien verursacht — wie an Abb. 2 ersichtlich — die weitgehende Verminderung der *Polyarthra platyptera* EHRBG. den Rückgang der Gesamtindividuenzahl. In der Tisza kommt die *Polyarthra platyptera* EHRBG. massenhaft vor: 4,600 Individuen/100 Liter, was 51% des Gesamt-Planktons ausmacht. Nach 5 km sinkt ihre Zahl von 4,600 auf 800 ab, was nur 14% des Planktons entspricht. Eine andere typische Rotatorienart ist *Keratella cochlearis* var. *tecta* GOSSE, deren Individuenzahl im Östlichen Hauptkanal einwärts schreitend ganz bis zuende gleichmässig zunimmt. Während in der Tisza 10 Individuen/100 L. zu finden sind, ist ihre Zahl im Kanal bei 40 km schon auf 780 gestiegen (Abb. 2.).

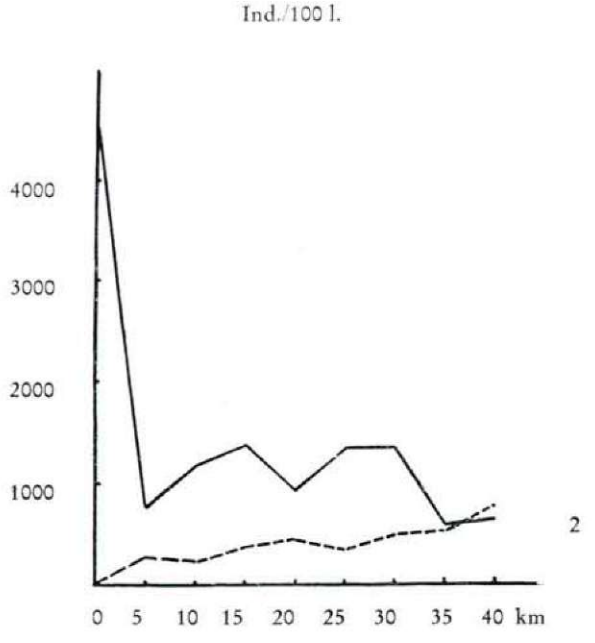

Abb. 2. 1. Keratella cochlearis v. tecta GOSSE
2. Polyarthra platyptera EHRBG.

Interessant gestaltet sich innerhalb der Crustaceen das Verhältnis zwischen *Nauplius*-Larven und ausgewachsenen Copepoden, welches Abbildung 3 darstellt. In der Tisza kommen sie in etwa gleicher Menge vor, während im Östlichen Hauptkanal die *Nauplius*-Larven stets in grösserer Zahl anzutreffen sind als die entwickelten Exemplare. In den meisten Fällen ist dort, wo die Zahl der *Nauplius*-Larven steigt, die der entwickelten Copepoden verringert und umgekehrt. Am ausgesprochensten zeigt sich dies bei 5 km, wo gegenüber

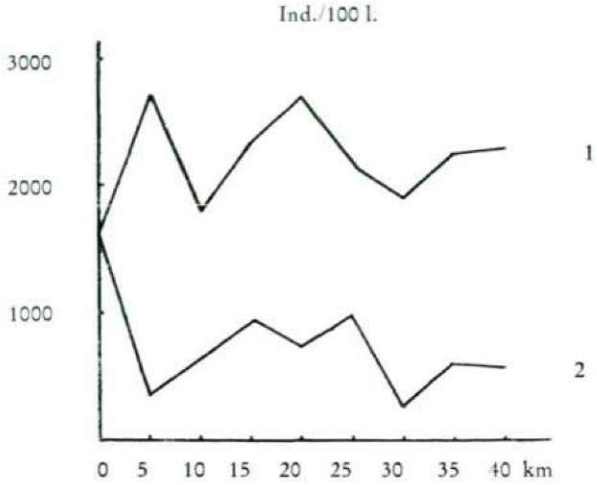

Abb. 3. 1. Nauplius-Larven,
2. Ausgewaschenen Copepoden.

Zusammenfassung

2,690 *Nauplius*-Larven insgesamt nur 370 ausgewachsene Individuen in 100 L Wasser zu verzeichnen waren.

Aus den Daten geht deutlich hervor, dass zu dem obigen Zeitpunkt das Zooplankton dieser Tiszastrecke und des Östlichen Hauptkanals sich vor allem in der Gesamtindividuenzahl unterscheidet. In der Tisza ist die Gesamtindividuenzahl beträchtlich höher als im Östlichen Hauptkanal. Bei den Protozoen sind wesentliche, das Gesamt-Zooplankton beeinflussende Veränderungen nicht eingetreten. Die Gesamtindividuenzahl der Rotatorien im Kanal ist im Verhältnis zur Tisza wesentlich verringert. Die Gesamtindividuenzahl der Crustaceen bewegt sich um die in der Tisza gefundenen Werte, sie ist um weniges geringer oder zuweilen mässig höher, aber im wesentlichen unverändert. Hier zeigt lediglich das Verhältnis von entwickelten Copepoden und *Nauplius*-Larven zueinander eine Abweichung (Abb. 3). Die grössten Abweichungen unter den Arten sind im Falle der *Polyarthra platyptera* EHRBG. zu beobachten, deren Individuenzahl im Östlichen Hauptkanal erheblich verringert ist.

Um ein volkommenes Bild über die Veränderungen des Zooplanktons im Östlichen Hauptkanal erhalten zu können, werde ich in Zukunft meine Untersuchungen durch Sammlungen zu solchen Zeiten erweitern, wo im Östlichen Hauptkanal der Durchfluss gering ist, sowie durch Sammlungen aus weiter von der Tisza entfernt gelegenen Abschnitten des Kanales.

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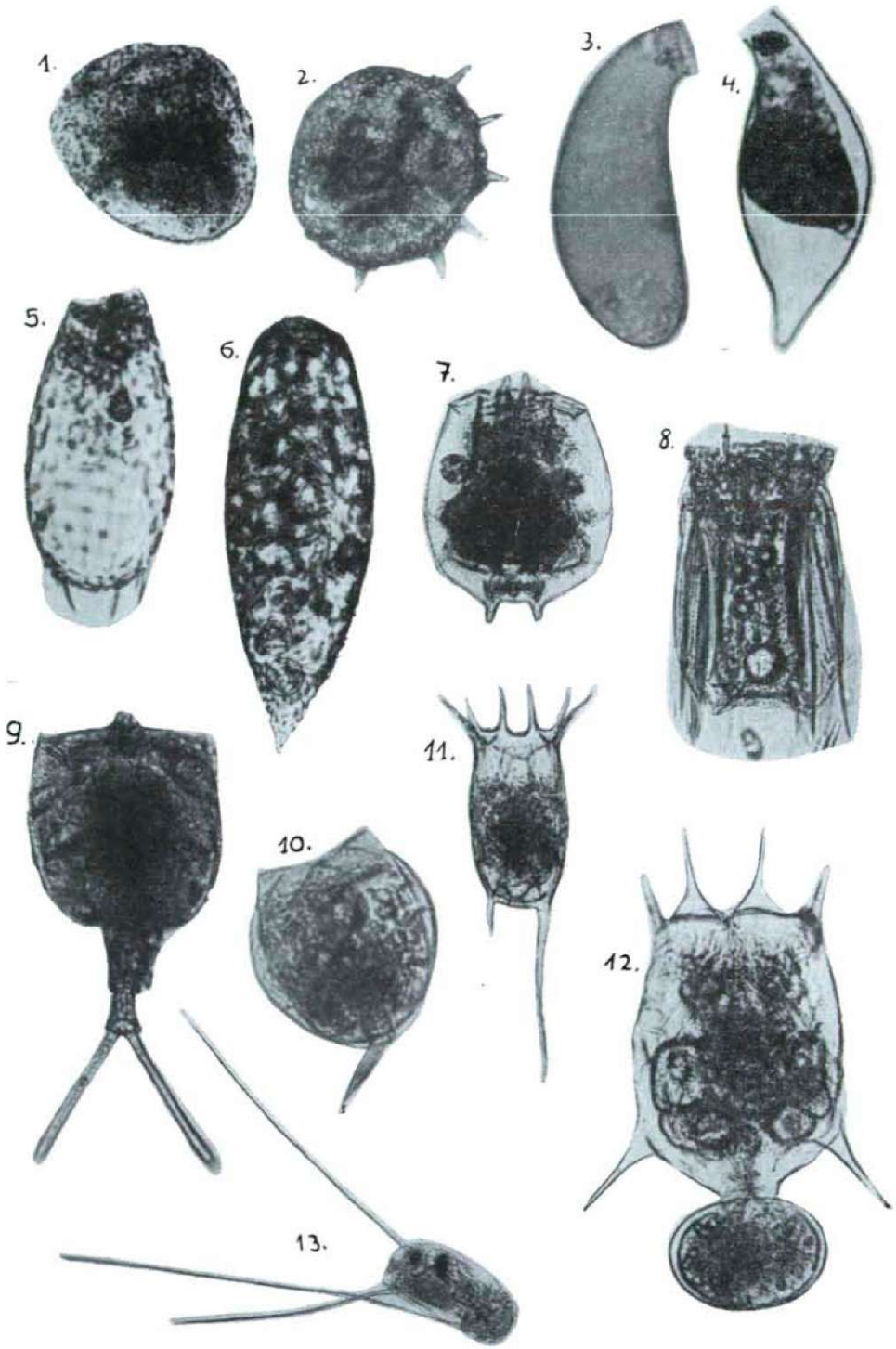
Tafelärklerung

1. Centropyxis constricta Defl.
2. Centropyxis aculeata Stein
3. Cyphoderia margaritacea Ehrbg.
4. Cypoderia trochus Penard
5. Euglypha sp.
6. Difflugia acuminata Ehrbg.
7. Brachionus angularis Gosse
8. Polyarthra platyptera Ehrbg.
9. Trichotria quadrangularis Stirnimann
10. Lecane luna O. F. Müller
11. Keratella quadrata v. valga Ehrbg.
12. Brachionus salyciflorus f. amphiceros Ehrbg.
13. Filinia longiseta Ehrbg.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	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%	ind/100 l	%
Protozoa																		
Arcella discoides EHRBG.			20	*0,34*	10	*0,22*	20	*0,33*									10	*0,17*
Centropyxis aculeata STEIN			110	*1,95*	10	*0,22*	20	*0,33*	20	*0,29*	20	*0,30*	20	*0,35*	30	*0,55*	30	*0,52*
Centropyxis constricta DEFL.			90	*1,57*	10	*0,22*	10	*0,16*	60	*0,90*	40	*0,62*			10	*0,17*	10	*0,17*
Difflugia gramen PEN.	10	*0,11*	10	*0,17*	10	*0,22*												
Difflugia lanceolata PEN.			70	*1,24*			20	*0,33*	60	*0,90*	20	*0,30*	60	*1,09*			20	*0,34*
Difflugia mammillaris PEN.			20	*0,34*														
Difflugia elegans PEN.			30	*0,52*														
Difflugia acuminata EHRBG.			10	*0,17*					20	*0,29*								
Difflugia amphora LEIDY													20	*0,35*				
Cyphoderia margaritacea EHRBG.			10	*0,17*			50	*0,83*	80	*1,20*	20	*0,30*	20	*0,35*			40	*0,71*
Cyphoderia trochus PEN.											20	*0,30*			10	*0,17*		
Euglypha alveolata LEIDY																	20	*0,34*
Euglypha brachiata LEIDY			10	*0,17*														
Euglypha sp.			30	*0,52*														
Codonella cratera LEIDY			10	*0,17*	10	*0,22*	40	*0,67*	40	*0,59*	100	*1,55*	20	*0,35*				
Vorticella sp.			10	*0,17*			10	*0,16*										
Ciliata sp.	390	*4,31*																
zusammen	**400**	*4,42*	**430**	*7,50*	**50**	*1,10*	**170**	*2,81*	**280**	*4,17*	**220**	*3,37*	**140**	*2,49*	**50**	*0,89*	**130**	*2,25*
Rotatoria																		
Filinia longiseta EHRBG.	60	*0,66*	240	*4,19*	240	*5,23*	200	*3,32*	280	*4,18*	360	*5,53*	460	*8,19*	290	*5,19*	350	*6,07*
Filinia terminalis PLATE					10	*0,22*											40	*0,71*
Polyarthra platyptera EHRBG.	4620	*51,20*	800	*13,99*	1150	*25,11*	1400	*23,24*	960	*14,34*	1360	*20,87*	1360	*24,19*	590	*10,59*	640	*11,10*
Polyarthra pl. var. *euryptera* WIERZ.					30	*0,65*												
Brachionus angularis GOSSE	130	*1,44*	320	*5,58*	110	*2,36*	190	*3,15*	280	*4,18*	240	*3,69*	280	*4,99*	210	*3,77*	270	*4,68*
Br. calyciflorus f. *amphiceros* EHRBG.			30	*0,52*	10	*0,22*	20	*0,33*	40	*0,59*	40	*0,61*			30	*0,53*	20	*0,34*
Keratella quadrata var. *valga* EHRBG.	50	*0,55*	180	*3,14*	110	*2,36*	140	*2,32*	160	*2,39*	20	*0,30*	20	*0,35*	40	*0,72*	70	*1,21*
K. quadrata var. *brevispina* EHRBG.							10	*0,16*										
K. cochlearis var. *irregularis* LAUT.	10	*0,11*	140	*2,45*	10	*0,22*	110	*1,82*	100	*1,49*			180	*3,22*	130	*2,33*	120	*2,07*
K. cochlearis var. *tecta* GOSSE	10	*0,11*	260	*4,55*	240	*5,23*	370	*6,14*	460	*6,87*	340	*5,21*	500	*8,89*	550	*9,87*	780	*13,52*
Euchlanis dilatata EHRBG.	10	*0,11*					10	*0,16*										
Lecane luna O. F. MÜLLER	10	*0,11*			20	*0,44*	10	*0,16*			20	*0,30*						
Monostyla lunaris EHRBG.			20	*0,34*														
Trichotria pocillum O. F. MÜLLER			10	*0,17*														
Trichotria quadrangularis STIRNIMANN															20	*0,35*	10	*0,17*
Asplanchna sp.	220	*2,43*							20	*0,29*					10	*0,17*	20	*0,34*
Synchaeta sp.	180	*1,99*	60	*1,04*	80	*1,75*	40	*0,66*	240	*3,59*	420	*6,44*	320	*5,69*	580	*10,39*	410	*7,11*
zusammen	**5300**	*58,71*	**2060**	*35,97*	**2010**	*43,79*	**2500**	*41,46*	**2540**	*37,92*	**2800**	*42,95*	**3120**	*55,52*	**2450**	*43,93*	**2730**	*47,32*
Crustacea																		
Bosmina longirostris O. F. MÜLLER			90	*1,57*	80	*1,74*	90	*1,49*	420	*6,26*	340	*5,21*	200	*3,55*	110	*1,97*	210	*3,63*
Chydorus sphaericus O. F. MÜLLER	10	*0,11*	10	*0,17*							20	*0,30*						
Copepoda	1650	*18,27*	370	*6,45*	630	*13,72*	930	*15,42*	740	*11,06*	980	*15,04*	260	*4,62*	600	*10,75*	590	*10,23*
Nauplius	1660	*18,38*	2690	*46,94*	1820	*39,65*	2340	*38,82*	2680	*40,00*	2160	*33,13*	1900	*33,82*	2230	*39,96*	2090	*36,23*
Ostracoda	10	*0,11*	30	*0,52*											130	*2,32*		
zusammen	**3330**	*36,87*	**3190**	*55,67*	**2530**	*55,11*	**3360**	*55,73*	**3840**	*57,32*	**3500**	*53,68*	**2360**	*41,99*	**3070**	*55,01*	**2890**	*50,09*
Sonstige Arten			50	*0,86*					40	*0,59*					10	*0,17*	20	*0,34*
zusammen	**9030**	*100*	**5730**	*100*	**4590**	*100*	**6030**	*100*	**6700**	*100*	**6520**	*100*	**5620**	*100*	**5580**	*100*	**5770**	*100*

MOLLUSCA-PERIODS IN THE SEDIMENTS OF THE HUNGARIAN PLEISTOCENE. III. THE UPPER HUMID PERIOD OF THE BORING OF FELSŐSZENTIVÁN

by

A. HORVÁTH

Institute for Systematic Zoology of the University, Szeged, Hungary

The second part of the work (Acta Biol. Szeged, 1963. Tom. IX. Fasc. 1—4, p. 101, 115) dealt with the sediments between 1,6—11 m of the boring of Felsőszentiván. This series of sediments was named by the author as the upper arid period and was shortly designated with the Roman numeral I. The period was divided into 8 subperiods (I./1—I./8) on the basis of the fauna. The I. period was characterized by the lack of aquatic fauna, by the sporadic occurrence of thermophilic species and by a more or less arid and cold climate.

Below the sediments of the I. period lies the upper humid period between 11 and 14,5 m. In contrast to the former period the aquatic and thermophilic fauna occurs in all samples of the period, the aquatic fauna is rich, the number of individuals of the thermophilic species is significant, the climate of the period is more humid and milder. The period is designated with II. and was divided into 4 subperiods (II./I.—II./4) on the basis of the fauna. Review of the period follows according to these subperiods.

Subperiod II./1. 11—11,6 m.

The layer is 60 cm thick. It consist of humus and mud containing loess with plant relics. In the three 20 cm thick samples in all 1725 *Mollusca* individuals were found. This subperiod sharply differs from subperiod I./8 through its fauna characteristic to the period II. and from the subperiod II./2 through its relative poor fauna.

The number of **aquatic species** is considerable, 7 from the 29 species of the subperiod. The number of individuals, however, belonging to these 7 species is only 70, hardly the 25th part of the total number of the *Mollusca* individuals. *Valvata pulchella* (22 pieces) is rare today on the Hungarian Plain; in this connection it may be considered as a nordic, oligothermic species. On the basis of its number of individuals it did not attain its optimum not even in this subperiod. But the high number of individuals shows a climate which was colder than that of today. *Anisus spirorbis* (20 pieces) is at present the most frequent aquatic snail of the Hungarian Plain. In the moun-

tains it is much rarer and it occurs in our loesses also rarer than at present. It is an enduring ubiquitous organism. In the relation of Pleistocene, however, it may be considered as an eurythermic thermophilic species. The moderate number of individuals may be attributed to a climate which was colder than that of today. *Anisus leucostoma* (15 pieces). On the Hungarian Plain it may be considered as an oligothermic species because it occurs more frequently in the loess than as recently. *Galba truncatula* (7 pieces). Also this species is more frequent in the loess, it is rather an eurythermic and oligothermic organism. *Anisus planorbis* (3 pieces) and *Valvata cristata* (2 pieces) are eurythermic species, but considering their optimum temperature they are somewhat polythermic. The low number of individuals may be attributed to the cold climate. *Pisidium cinereum* (1 piece) is an enduring ubiquitous organism. At present it is a very frequent species on the Hungarian Plain. The lack of *Bithynia tentaculata, Limnaea stagnalis* and *Radix ovata* — which are much rarer in the Pleistocene — emphasises the Pleistocenous character of the coenosis. Number of individuals of the aquatic species diminishes upwards from below (34, 24 and 12 resp.). The number of species does not show this downward tendency; 6 species from the 7 species of the subperiod occur in the uppermost boring-sample too. The diminishing is not parallel with the sequence in the tolerancy of desiccation; in the uppermost sample the number of the desiccation mostly tolerating *Anisus spirorbis* considerable diminishes and at the same time the bi branchiate aquatic snails of the subperiod occur too. On this basis the water seems a permanent one. The poor fauna may be attributed to the low temperature of the water while the diminishing of the number of individuals may be explained by the increase of cold and aridity and by the fall of the water. Entire and permanent ceasing of the aquatic fauna above the subperiod indicates the drying up of the water and the beginning of the upper arid period.

The 308 individuals of the **amphibic** category are distributed into 2 species. Number of individuals of *Succinea oblonga* (281 pieces) is considerable lower than in the neighbouring periods I./8 and II./2. This may be explained by the low temperature and humidity. *Carychium minimum* (27 pieces) is lacking in the period I. while it occurs continuously in the period II. Its occurrence is simultaneous with the aquatic fauna although in a humid biotop it subsists also far from the water. It is an eurythermic organism. The southern form (subsp. *tridentatum* Risso) is not known from the boring of Felsőszentiván. Recently, however, this subspecies occurs in Middle-Europe too.

In the subperiod the most populous group is that of the **terrestric ubiquitous** organism (11 species and 1093 exemplars). This fauna is similar to the fauna of the lowest subperiod of the upper arid period (I./8). As comparison, behind the quantitative data of the species, author gives also the qualitative data of the 3 lowest samples of the subperiod I./8 drawn together in parentheses. These numbers refer to identical quantity of the samples. *Pupilla muscorum* 306 (333) exemplars. It is more resistant against cold and aridity than the other ones. It is the preponderantly dominant species in both subperiods. The quantitative differences in the number of individuals, taking into consideration the differences between the single samples, are unimportant. It may be supposed that the humidity with low temperature of these subperiod was a little disagreable for it. *Trichia hispida* 118 (258) exemplars. The decrease of quantity is considerable. It is the most frequent snail of the Hungarian Plain. It is resistant against

cold or most correctly it may be considered as a cold-lover, because it rambles even on winter-days. Its demand on humidity is considerable but at low temperature it is satisfied with lower humidity too. the decrease may be due to the effect of cold humidity. *Vertigo pygmaea* 214 (12), *Vallonia costata* 174 (15), *Vallonia pulchella* 91 (14), *Cochlicopa lubrica* 66 (23), *Vallonia enniensis* 54 (3), *Deroceras agreste* 32 (21), *Vitrea crystallina* 17 (6) occur continuously in the subperiod I./8 too, but the number of individuals is there much lower. They are small, against cold and aridity resistant and from before unfavourable conditions easily hiding organism. Increase of number may be due to the rising of humidity and warmth. Rising of temperature is proved by the considerably increased number of individuals of the rather thermophilic *Vallonia enniensis* and of the eurythermic but rather thermophilic *Vallonia costata*. It is to be noted that the sequence of the *Vallonia* species adjusts itself to the cold-resistance and not to the thermophily. Predominance of *Vallonia costata* is due to its highest cold-resistance. The number of indviduals of these species show, however, more or less unfavoŭrable conditions, not because humidity was low, but because warmth was lacking. *Vertigo angustior* (10) does not occur in the upper arid period. It appears first in the subperiod II./1 and from here downwards it occurs continuously. It is sensitive to great coldness. Its appearence shows the increase of temperature but this increase was not a great one which shows the low number of individuals. *Punctum pygmaeum* too occurs from here downwards continously. In the upper arid period only 3 exemplars of this species were found. On the Hungarian Plain it is an oligothermic species. Its appearence and survivance is due mostly to the increase of humidity.

Inhabitants of groves are represented by 6 species and 76 individuals. *Perpolita hammonis* (55 exemplars) occurs continuously both upwards and downwards. Number of individuals upwards diminishes and downwards increases. The increase indicate the rise of humidity, vegetation and temperature. In Hungary it is an inhabitant of mountains, and on the Hungarian Plain it may be considered as an oligothermic species. It lives permanently next to waters, the low number of individuals is caused therefore not by the lack of water but by the low temperature. This show a climate which was much colder than at present. *Fruticicola fruticum* (13 exemplars). In the upper arid period it was not found, in this period it occurs downwards continually from the beginning. This snail is considerably large and therefore the low number of individuals found in the small boring-samples does not prove its rarity. Its constant occurence show rather a frequent occurence. It is an important element of the *Mollusca* fauna of North-Europe. It shows a preference for groves. *Arianta arbustorum* (2 exemplars). In the boring of Felsőszentiván it occurs first in the upper sample of this subperiod. Three samples deeper from the beginning of the subperiod II./2 it occurs downwards continually. Its distribution and its requirements are similar to them of the former species. The occurence of both species proves the increase of humidity and vegetation. They prefer first of all the groves with deciduous trees and their occurrence makes probably the presence of such vegetation. Besides they occur in pine-woods and above the timber line in low vegetation too. On the Hungarian Plain they are oligothermic species and they indicate a climate which was colder than at present. *Goniodiscus ruderatus* (2 exemplars). In the profil this

species too appears first in the upper sample of the subperiod II./1. In the other two samples of the subperiod it is lacking, while from the subperiod II./2 downwards it occurs continually. In Hungary it is a sporadic and oligothermic inhabitant of mountains. It is a frequent species in North-Norway. Its occurrence in the subperiod proves a much colder climate than at present and it makes probably the occurrence of groves. *Perforatella bidens* (1 exemplar). In the profil it appears with the two former species and its further occurrence is also similar. It is sensitive to great coldnes but here it proves a climate colder than that of today. Its occurrence indicates much humidity and the presence of deciduous groves, although it occurs in low vegetation too. *Pupilla sterri* (3 exemplars). It occurs only in the upper sample as the last case of its continuous occurrence in the upper arid period. It prefers the moderately cold and arid climate, its disappearence is comprehensible in the cold and humid climate. At present it is an inhabitant of rocks in the mountains. Its occurrence undoubtedly proves a climate which was colder than the present one.

Three species and 178 individuals of the **thermophilic organisms** were found. *Imparietula tridens* (115 exemplars). Its continuous occurrence begins already in the subperiod I./8. But there were found only 18 exemplars in the 5 samples. The number of individuals considerably increases in the subperiod II./1, its occurrence continues in the subperiod II./2 with a smaller number of individuals. The inconsiderable increase of number is due to the warmth and not to humidity. It indicates a climate which was much warmer than of the subperiod I./8. Besides it occurs also on humid places if they have a sufficiently warm microclimate. It is therefore understandable that in the subperiod this is the dominant thermophilic species. *Abida frumentum* (61 exemplars). In the profil it appears first in the upper part of the subperiod II./1 and downwards it occurs continually beyond the subperiod too. Its requirement for warmth is greater than that of the former species. It avoids the humid places in consequence of their cold microclimate. It indicates a considerable warmth but it does not preclude a climate which was colder than at present. *Helicella hungarica* (2 exemplars). It occurs here only in the upper sample. In the lower part of the subperiod I./8 it occurs continuously, although only in small numbers. Below the subperiod II./1 it occurs also discontinuously. Its requirement for warmth is higher than that of the former species, it avoids more humid places. The number of individuals here is due to humidity.

The **oligothermic** *Vallonia tenuilabris,* which occurs at present only in Asia, is here lacking, although it occured continuously in the subperiod I./8. This disappearence indicates rise in temperature.

On the basis of the foregoing the following **reconstruction of the circumstances** may be given. The climate of the subperiod was much warmer and more humid than that of the subperiod I./8, and considerable colder and arider than the present climate of the Hungarian Plain. On the area there was a cold standing water which gradually diminished due to the insufficient quantity of rainfall. Its desiccation was delayed through low temperature. The vegetation was steppe-like with groves on the shores. In the groves occured possibly cold-resistant deciduous trees (probably *Betula, Alnus, Salix* etc.) besides pines.

Subperiod II./2. 11,6—12,4 m.

This layer is 80 cm thick. It consists of humus and mud containing loess and includes plant residues. The lowest sample (12,2—12,4) consists of running sand. The subperiod may be clearly distinguished from subperiod II./1 through a richer and from subperiod II./3 through a poorer fauna. In the subperiod altogether 10 584 exemplares were found. Number of species was 42 (in the subperiod II./1 only 29!). The **aquatic fauna** is represented by 18 species and 954 individuals. The species of the subperiod II./1 occur also here but the number of individuals are much higher. In low numbers occur further 11 species. The great majority of individuals (601) belong to such 7 species which are on the Hungarian Plain more frequent in loess as recently and therefore they may be considered as oligothermic organism. These species are as follows: *Anisus leucostoma* (408 exemplars), *Galba truncatula* (117 exemplars), *Valvata pulchellla* (40 exemplars), *Gyraulus laevis* (18 exemplars), *Pisidium obtusale* (9 exemplars), *Aplexa hypnorum* (5 exemplars), and *Bithynia leachi* (4 exemplars). A climate which was colder than at present is proved by the dominance of *Anisus leucostoma* and by the high number of *Valvata pulchella.* The Pleistocene character of the fauna is underlined also by the continuous occurrence of *Gyraulus laevis* which has a holarctic distribution but is generally infrequent at present.

The other individuals represent mostly eurythermic species which are frequent recently and in the loess as well. In Hungary they occur rather on the plains than in the mountains. They may be considered here as a slightly polythermic organisms. These species are the followings: *Anisus spirorbis* (3198 exemplars), *Anisus planorbis* (56), *Valvata cristata* (33), *Planorbis corneus* juv. (5), *Anisus vortex* (1); altogether 5 species and 293 individuals. Number of individuals was diminished probably by a climate colder than at present.

The eurythermic and ubiquitous *Pisidium cinereum* (46 exemplars) proves only the presence of water.

The polythermic aquatic fauna (which may be considered as such in the Hungarian Pleistocene) is represented by 5 species but only by 14 individuals. *Anisus septemgyratus* (9 exemplars) is in the loess locally frequent, but at present it occurs northwards only as far as Germany and Middle-Russia. Its presence therefore excludes a very cold climate. *Physa fontinalis* (2 exemplars), *Bithynia tentaculata* (1) and *Segmentina nitida* are in Hungary more the inhabitants of the plains than that of the mountains. In the loess they are rarer than recently. Their occurrence and especially their joint occurrence proves a climate which was milder than that of the subperiod II./1. Their low number proves a colder climate than at present. *Anisus carinatus* (1 exemplare) is in Hungary equally rare, recently and int the loess as well. Its distribution shows a preference for oceanic climate, which is in comparison with the climate of the Pleistocene mild and humid and in comparison with the present climate of the Hungarian Plain cool and humid.

The aquatic fauna of the subperiod is the richest in the third sample from above (12,0—12,2 m). Upwards it diminishes fast and steadily. This proves that the water gradually diminished because the rainfall could not entirely substitute for the loss of water through evaporation. The considerably evaporation indicates a climate with relatively warm summers. In the Holocenous

climate several standing waters came into existence on the Hungarian Plain; the climate of the subperiod was therefore arider.

The **amphibic fauna** is represented by *Succinea oblonga* (2803 exemplars) and *Carychium minimum* (600), altogether 3403 individuals. They occur from the subperiod II./1 continuously. The high increase of the number of individuals is due to the increase of temperature and humidity. In the upper three samples the gradual decrease of the aquatic fauna is shown also by the amphibic organism. The immediate cause of the decrease of number of individuals is here not the decrease of the water itself but the decrease of the humidity of the shores. This latter, however, may be explained similarly as the decrease of the water.

The **hygrophilic terrestric ubiquitous** organisms are represented by 13 species and 5 777 individuals. The species, which occured already in the subperiod II./1, occur here generally in higher number; increase of temperature and humidity was favourable for all species. The changes of the environmental factors were, however, differently advantageous for the different species. The sequence of the species is therefore an other than in the subperiod II./1. *Vallonia pulchella* (1 525 exemplars) forges ahead from the fifth place. *Pupilla muscorum* (1 125 individuals) is here the second. In the subperiod II./1 it was the first. A greater number would be found if the area were a little arider. *Vertigo pygmaea* (1112 exemplars). Its conditions of living became more advantageous. It follows also here *Pupilla muscorum. Vallonia enniensis* (757 exemplars). It is here the forth; in the subperiod II./1 it was the seventh. It is a rather thermophilic organism. Increase of number indicates a considerable increase of temperature. *Vallonia costata* (307 exemplars). In the subperiod II./1 it was the fourth, here it is the fifth. Increase of its number in the two upper samples is rather considerable. In the two lower samples its quantity is similar to that of the subperiod II./1. A greater degree of multiplication was hindered by the temperature which was lower than its optimum. *Trichia hispida* (299 exemplars). Before, it was the fourth. Here, it is the sixth. Increase of numbers indicates more favourable conditions. This increase may be attributed to the rise of temperature of the humide water-shores. Increase of number of *Cochlicopa lubrica* (264 exemplars) may be explained by the same cause. Increase of number of individuals of the relatively thermophilic *Vertigo angustior* (152 exemplars) proves the increase of temperature. The conditions for livings of *Deroceras agreste* (126 exemplars) became considerable more favourable while them of *Punctum pygmaeum* (44 exemplars) and *Vitrea crystallina* (27 exemplars) did not change very much. These two latter species are on the Hungarian Plain at present oligothermic species. *Euconulus trochiformis* (22 exemplars) occurs continuously but only in low number. It did not occur in the subperiod II./1. It is resistant to cold but at the same time it requires humidity. Its presence here proves the increase of humidity. *Vertigo antivertigo* (17 exemplars) appears first here in the boring. It requires more warmth and humidity than *Vertigo pygmaea.* Its quantity is therefore insignificant as compared to the other species. Its presence indicates a temperate cold and more humidity.

Similar ubiquitous populations are found at present in the lower parts of our mountains on shores in the rich vegetation and in the plant debris. The population proves much humidity and a great degree of covering by plants.

It excludes a very cold climate and makes probably a climate which is colder than that of the Hungarian Plain at present. This climate was, with all probability, moderately cold.

Six species and 237 individuals of the **inhabitants of groves** were found. Number of species is the same as in the subperiod II./1. 5 species of the six occur in both subperiods. Dominant is also here *Perpolita hammonis*. Number of individuals is here increased. Increase of number of *Perforatella bidens* (53 exemplars) is the highest. This species is oligothermic in a lower degree than the former one. Its occurrence indicates a considerable increase of temperature. *Arianta arbustorum* (28 exemplars) occurs here in greater number. This is a little oligothermic species. *Fruticicola fruticum* with a similar requirement is represented by 17 individuals only. Number of the considerable oligothermic *Goniodiscus ruderatus* (11 exemplars) is also increased, its occurrence became continuous but the number of individuals remains low. *Clausilia dubia* (1 exempl.) appears only here in the whole upper humid period. In Hungary it is at present an inhabitant of the mountains and in the boring indicates a climate which was colder that at present. *Pupilla sterri* (1 exemplar) occurs only in the uppermost sample of the subperiod II./1. It may be supposed that it is lacking here because of the cool humidity.

The grove-inhabitant population described above proves a climate which was colder, than that of today and it proves also a great covering degree of the vegetation. Some of the species occur on places with open vegetation too but the occurrence of the whole population in open vegetation is improbable. Presence of groves is made probable by the rather rich ubiquitous fauna and by the continuous presence of water too. Pinewood is not liked by snails because of the unfavourable mechanical properties of the fallen pine-needles. Author found rather rich populations along the torrents of the Alpes in *Piceetea* but the population of the subperiod fits better into deciduous groves than into pine-woods. On the basis of the climate reconstructed with the aid of the fauna and on the basis of his personal experiences author thinks that the vegetation of this subperiod was similar to that of the subperiod II./1, i. e. it was a vegetation from cold-resistant deciduous trees.

The **thermophilic organisms** are represented by 3 species and 213 individuals. Comparing with the subperiod II./1 the value of the "thermophilic species altogether" shows a considerable rise in the second sample, while in the upper sample a little, in the lower one a very considerable diminishing may be observed. From the 3 species *Abida frumentum* (129 exemplars) is the first. This species has an intermediate position from the point of view of thermophily. Its great quantity in the second sample (11,8—12,0 m) is very remarkable and indicates that this sample was the warmst point of the whole period. In the upper sample it occurs in a much lesser quantity, although this is yet more than the quantity in the subperiod II./1. In the two lower samples the quantity is considerable smaller than in the subperiod II./1. *Imparietula tridens* (76 exemplars) occurs in relatively great number, but this quantity is in the two upper samples a little, in the two lower samples considerable smaller than in the subperiod II./1. The most thermophilic *Helicella hungarica* (8 exemplars) proves in the two upper samples a warmth higher than that of the subperiod II./1. In the two lower samples it lacks almost entirely. A climate which was warmer than that of the subperiod II./1. is proved therefore by the thermophilic fauna of the

two upper samples too. In the two lower samples, on the basis of the thermophilic fauna, the contrary might be concluded. From the analysis of the other parts of the fauna, however, is clear, that the climate was also here warmer. The smaller number of the thermophilic organisms is due here to the humidity.

On the basis of the analysis of the fauna **the climate of the subperiod II./2** was milder and more humid and colder and more arid than the climate present. Generally this climate was moderately cold and rather humid. The cold is caused by the cooling effect of the moderately thick inland ice-cover in Scandinavia. On the area there was a standing water which, in consequence of the arid and relatively warm summers, gradually diminished. On the shores there were cold-resistant deciduous groves. From the point of view of natural surroundings the subperiod was inhomogeneous. In the lowest sample the fauna is the fifth of that of the uppermost sample of the subperiod II./3. This change indicates the beginning of an arid and continental climate. The summers were mildered in consequence of the inland ice-cover and the colder winters were unfavourable for the fauna. The following sample shows the increase of humidity and warmth. The increase of temperature was caused by the foregoing of the evolution of the climate-type and the diminishing of the ice-cover. The increase of humidity originated rather from the melting of ice than from the rainfall. The fauna of the subperiod is here the richest. In the following sample the aquatic fauna considerably diminishes and diminishes also the terrestric fauna. The thermophils, however, have here a peak. The warm and arid climate-type here is the most expressed. In the upper sample the aridity increases and at the same time the temperature diminishes.

Subperiod II./3. 12,4—14,0 m.

This layer is 160 cm thick. It consists of running sand. Two samples of 20 cm and four samples of 30 cm belong to this subperiod. Its rich fauna clearly distinguishes it from the subperiods above and below. Number of species is 50, number of individuals 51 379.

The **aquatic fauna** is represented by 25 species and 11 999 individuals. The three groups, which was distinguished in the case of the subperiod II./2 are found also here. The group of the slightly polythermic organisms is here the first and not the second. Number of species belonging to this group is 8, that of the individuals 7567. Their distribution is the following: *Anisus spirorbis* 6405, *Anisus planorbis* 576, *Valvata cristata* 484, *Stagnicola palustris* 43, *Planorbis corneus* 29, *Gyraulus crista* 22, *Valvata piscinalis* 7, *Gyraulus albus* 1. Dominant is *Anisus spirorbis;* the number of individuals belonging to this species is more than the half of the number of all aquatic organisms. The sequence of the species which occur in this subperiod and in the subperiod II./2 as well is the same in both subperiods, the number of individuals, however, is much higher. *Stagnicola palustris,* which was lacking in the subperiod II./2, has here the fourth place; therefore *Planorbis corneus* has here the fifth place. *Gyraulus crista, Valvata piscinalis* and *Gyraulus albus* appear in the period first here, but only in low number. *Anisus vortex* was not found here; in the subperiod II./2 was found only 1 exemplar.

The oligothermic group is represented by 11 species and 3 850 individuals. Their sequence is as follows: *Galba truncatula* 2060; *Valvata pulchella* 862,

Anisus leucostoma 616, *Aplexa hypnorum* 92, *Gyraulus laevis* 91, *Bithynia leachi* 88, *Pisidium obtusale* 22, *Pisidium personatum* 14, *Bathyomphalus contortus* 3, *Pisidium pulchellum* 1, *Pisidium nitidum* 1. This group has here the second place, but it has a significant role. In the quantitative sequence of the aquatic organisms the second, third and fourth place take the members of this group *(Galba truncatula, Valvata pulchella, Anisus leucostoma).* It indicates an increase of temperature that the only slightly oligothermic *Galba truncatula* predominates, while the considerably oligothermic *Anisus leucostoma* loosing its first place became the third. Increase of number of *Valvata pulchella* and the locale increase of number of individuals of oligothermic organisms, especially in the upper part of the period, prove a cold climate after all. The species of the oligothermic group found in the subperiod II./2 occur also in this subperiod. *Bathyomphalus contortus, Pisidium personatum, Pisidium pulchellum* and *Pisidium nitidum* appear first here in the period, but only in insignificant numbers and in the sequence they have the four last places. *Pisidium pulchellum* and *Pisidium nitidum* are in Hungary rare, recently and in the Pleistocene as well.

Increase of number of individuals of the eurythermic *Pisidium cinereum* (553 individuals) is very considerable.

The polythermic aquatic fauna is represented by 5 species and only 29 individuals. The continuous occurrence of *Anisus septemgyratus* excludes a great coldness, the low number of individuals shows a climate which was colder than at present. Increase of number of *Segmentina nitida* (9 exemplars) shows perhaps a slight increase of temperature. *Anisus carinatus* (5 exemplars) occurs only in the uppermost and lowest samples. *Viviparus viviparus* (2 exemplars) appears only in those two samples where the considerable increase of the aquatic fauna indicates an increase of the water too. *Valvata piscinalis* (see in the group of the slightly polythermic organisms) was found in the same two samples. This organism prefers the clear water. *Physa fontinalis* (1 exemplar) was insignificant as well as in the former subperiod. *Bithynia tentaculata* was not found; in the subperiod II./2 was found only one individual.

In this subperiod the aquatic fauna found more favourable conditions than in the subperiod II./2. The increase of the number of slightly polythermic organisms against the oligothermic ones and the dominancy of the slightly oligothermic *Galba truncatula* among the oligothermic organisms indicate the rise of temperature. Change of climate, however, was favourable for the oligothermic organisms too, though only in a smaller degree. This is proved by the locally considerable increase of number of individuals. The climatic change did not influence the polythermic organisms. Their role is insignificant as in the subperiod II./2. The value of the „aquatic species altogether" shows a considerable rising tendency. A relapse may be observed only in the third sample (from below) and in the uppermost sample. This latter is, however, in the neighbourhood of the subperiod II./2 and the relapse is therefore naturally. According to all these, the quantity of water was increased by the rainy climate and by the melting of ice. This excludes the presence of arid and warm summers and proves an oceanic climate with mild winters. The aquatic fauna observed fits into this moderately cold climate with mild winters.

The category of **amphibic organisms** is represented also here by *Succinea oblonga* (14447 exemplars) and *Carychium minimum* (1141 exemplars). This great increase proves the increase of the humidity with favourable temperature

of the shores and its fluctuations as well as the aquatic fauna proves that of the waters. *Succinea oblonga* is already rare above the 60 degree of latitude. Where it occurs in such a great quantity, the climate could not be a very cold one.

The fauna of the **hygrophilic ubiquitous organisms** is similar to that of the subperiod II./2. The same 13 species were found here too. The number of individuals increased considerably, it was 19956 in all. *Vertigo antivertigo* occurred only in the two lowest samples of the subperiod II./2; here it occurs continuously and the number of individuals too is rather high. The other species occur also continuously, as in the subperiod II./2; only *Vitrea crystallina* is lacking in two samples. The quantitative sequence of the species is the following: *Vallonia enniensis* (6254 exemplars). It gets the first place (before it was the fourth), although it dominates only in two samples. The great increase in number indicates humid and mild surroundings. *Vertigo pygmaea* (5706 exemplars). The same favourable effects promoted it from the third place to the second one. It dominates in the three lower and in the uppermost samples, where the colder climate was more favourable for it than for the more thermophilic *Vallonia enniensis*. *Vallonia pulchella* (3140 exemplars) is forced to the third place from the first one, although the conditions of living remain favourable for it. It is not a dominant in the samples but in the two lower samples it precedes the more thermophilic *Vallonia enniensis*. *Pupilla muscorum* (861 exemplars) has here the fourth place instead of the second one. Conditions of living were most favourable in the subperiod II./2 because of the more warmth in summer. *Euconulus trochiformis* (782 exemplars) is a good cold resistant organism but it is hygrophilic too. The number of individuals is considerably increased. Cold-resistance and requirement of humidity of *Cochlicopa lubrica* (755 exempl.) and *Deroceras agreste* (654 exemplars) is considerable. Number of individuals of these two latter species is increased in the three upper samples, downwards this number is slightly, and in the lowest sample considerably diminished. *Vertigo angustior* (554 exemplars). In the Pleistocene it was a thermophilic species. The conditions of life were in three of the six samples umchanged, while in the other three samples these conditions became considerable favourable in consequence of mild humidity. *Trichia hispida* (478 exemplars). Increase of its quantity in the uppermost sample is very considerable. It may be found in great quantity recently in the mountains, on lower places, next to water in humid surroundings. In the uppermost sample the microclimate was similar. In the following too samples the number of individuals is similar to that observed in the subperiod II./2, while in the three lower samples the number considerably diminishes. For this species it would be perhaps favourable more warmth in the humid second sample while more aridity in the colder climate of the lower samples. The mild humidity was favourable for *Vertigo antivertigo* (446 exemplars). For the more thermophilic *Vallonia costata* (276 exemplars) were the warmer summers of the subperiod II./2 more favourable than the mild winters of this subperiod. The conditions of life for *Punctum pygmaeum* (38 exemplars) and *Vitrea crystallina* (12 exemplars) changed only slightly. After all, this group indicates a similar climate in the terrestric biotops as the aquatic fauna in the water. On the basis of the snail-population a high covering degree of the vegetation may be supposed.

Number of species of the **inhabitants of groves** is 6, similarly to the subperiod II./2; number of individuals is 663. *Perpolita hammonis* (408 exemplars)

is also here dominant. Its quantity increases considerably in the two upper samples. In the two following samples its quantity is about the same as in the subperiod II./2. In the two lower samples its quantity is considerably diminished. The conditions for *Arianta arbustorum* (106 exemplars) became more favourable. *Pupilla sterri* (64 exemplars) indicates a climate which was colder than that of today. This organism is lacking in the subperiod II./2. The conditions for *Perforatella bidens* (52 exemplars), *Fruticicola fruticum* (18 exemplars) and *Goniodiscus ruderatus* (15 exemplars) did not change essentially. *Clausilia dubia* is lacking; in the subperiod II./2 was found only 1 exemplar. As compared with the subperiod II./2 the conditions for the fauna were in four samples more favourable while in two samples less favourable. The advantages of the mild and humid climate are shown therefore on the inhabitants of groves too.

The 3 **thermophilic species** occurring in the subperiod II./2 are found also here. Number of individuals is 160 in all. In contrast to the former subperiod here *Imparietula tridens* (124 exemplars) is the dominant. This species may be found mostly on more humid places. The condition for it were in the two upper samples more favourable than in the former subperiod. In the three lower samples the conditions were more disadvantageous than in the former subperiod, possibly in consequence of the cold and humid surroundings. *Abida frumentum* (26 exemplars), which prefers arider places in consequence of its thermophily, has in the two upper humid samples only a small role, in the lower samples it just occurs. The most thermophilic *Helicella hungarica* (10 exemplars) is here so subordinant as in the subperiod II./2. The differences between the subperiods II./2 and II./3 are caused by the cooler and more rainy climate of the latter.

In the uppermost sample the **oligothermic** *Vallonia tenuilabris* (3 exemplars) indicates a colder climate than that of today but at the same time the low number of individuals shows, that the cold was not a very strong one.

On the basis of the data above **the climate of the subperiod** II./3 was of a more oceanic type, more humid, with cooler summers and milder winters than the climate of the subperiod II./2. This climate was colder than that of today, after all it was moderately cold which was caused probably by the cooling effect of the inland ice-cover in Scandinavia. On the area there was standing water. The quantity of this water was twice considerable increased by rainfall and by melting of ice. On the shores there was a rich vegetation, possibly from cold-resistant deciduous trees. In the lowest sample the change of climate is indicated by the general and considerable increase of the fauna. In the following sample the fauna increases in consequence of increase of humidity. According to authors supposition, increase of humidity was caused in first line by the melting of ice in consequence of the mildering of climate and not by rainfalls. In the following sample the fauna became poorer in consequence of the decrease of humidity. This decrease is caused probably by the slowing of the melting process. In the two following samples the humidity and the temperature considerably increase. The causes of these changes were probably the gradual evolution of the climate-type and also the decrease of the inland ice-cover in Scandinavia. In the upper sample the considerable diminishing of the fauna is caused by the neighbouring climate-type. But the fauna is yet rich enough for a clear distinction from the subperiod II./2. These changes are unambiguosly indicated by the categories of the aquatic, amphibic, hygrophilic terrestric ubiquitous and groves inhabitant organisms.

Subperiod II./4. 14,0—14,5 m.

This layer is 50 cm thick. It consists of running sand. A sample of 30 cm and an other of 20 cm were investigated. Number of species is 27, that of the individuals 601. The subperiod may be clearly distinguished by the fauna which is upwards much richer and downwards much poorer. The data „*Mollusca* exemplars altogether" of the middle arid period bordering downwards this subperiod are the followings: 33, 38, 15, 54, 39 etc. In the subperiod II./4 the **aquatic fauna** is represented by 10 species and 126 individuals only. Disregarding from the considerable impoverishment, the fauna is similar to that of the subperiod II./3. Here is the slightly polythermic eurythermic group the dominant one. It is stricking the superiority of *Anisus spirorbis* (77 exemplars). The number of individuals of the other species is small: *Valvata cristata* 7, *Anisus planorbis* 6, *Stagnicola palustris* 3, *Planorbis cornea* 1. Three species, which occurs in the subperiod II./3 in the lowest numbers, here are lacking.

From the oligothermic group (4 species and 23 individuals) occurs also here *Galba truncatula* in the highest number (15), and follows also here after *Anisus spirorbis*. The number of individuals of the other species is small: *Valvata pulchella* 4, *Gyraulus laevis* 2, *Pisidium obtusale* 2. Number of the species decreased with 7, but from these occured 4 in the subperiod II./3 only in small number.

The polythermic group is lacking. But its quantity was also in the subperiod II./3 insignificant. From these changes a more arid and colder climate may be supposed.

The category of **amphibic organisms** is represented by 133 *Succinea oblonga* and by 59 *Carychium minimum*, in all by 192 individuals. All two species occurs continuously from above. The considerable decrease of their number is due to the arider and colder climate.

The **hygrophilic ubiquitous organisms** are represented by 12 species and 271 individuals. *Vitrea crystallina* did not appear, it occured however, in the subperiod II./3 in the lowest number too. The other species are common with the subperiod II./3, its quantity, however, is much reduced. The sequence is the following: *Vertigo pygmaea* 79, *Vallonia pulchella* 69, *Vallonia enniensis* 56, *Cochlicopa lubrica* 16, *Vertigo angustior* 11, *Pupilla muscorum* 9, *Deroceras agreste* 8, *Trichia hispida* 8, *Vertigo antivertigo* 6, *Euconulus trochiformis* 5, *Vallonia costata* 3, *Punctum pygmaeum* 1 exemplars. The dominant species are also here the same which were the dominants in the subperiod II./3. The quantity of the other species is also here much smaller. *Vallonia enniensis* gets here the third place instead of the first. This indicates the decrease of temperature, the high number of individuals, however, shows only a temperate cold. On the first place *Vertigo pygmaea* is found. This is not very stricking, because it was in three samples of the subperiod II./3 the dominant species. The dominancy of this species too indicates the temperateness of the cold. The more cold-resistant *Vallonia pulchella* precedes *Vallonia enniensis*. The fauna, after all, is similar to that of the subperiod II./3. It indicates, however, an arider and colder climate and the decrease of vegetation.

From the group of the **inhabitants of groves** only *Arianta arbustorum* (4 exemplars) and *Perpolita hammonis* (3 exemplars) were found. The cause of this considerable reduction was probably the decrease of humidity and vege-

tation. Decrease of temperature is indicated mostly by the disappearence of *Perforatella bidens.*

The decrease of the quantity of the **thermophilic organisms** was also considerable. Only *Imparietula tridens* was found, but only in small quantity (5 exemplars). The two other more thermophilic species are lacking. This indicates a considerably decrease of the temperature.

On the basis of the above data **the climate of this subperiod** was much arider and colder than that of the subperiod II./3. The climate was, however, in the Pleistocene only moderately cold. The vegetation get a steppe-like character. The presence of thickets on the shores, however, may not be excluded. The inland ice-cover in Scandinavia was thicker.

The upper humid period and the chronology of the Pleistocene

Author makes an attempt at the placing of the upper humid period into the stratigraphical and into the astronomical chronology. At the beginning, he investigates the two chronology separately from the point of view of the *Mollusca* fauna.

1. The stratigraphical chronology. The boring of Felsőszentiván was conducted by Prof. MIHÁLTZ, a stratigraphical profil and the stratigraphical chronology was completed by him. The stratigraphical data in authors's series of articles were taken from him. Author's task in this chapter is a control of MIHÁLTZ's stratigraphical chronology on the basis of faunaanalysis. Considering the three loess layer of the upper arid period from above as Würm 3, Würm 2 and Würm 1 and the separating running sand layers as the corresponding interstadial periods, the upper humid *Mollusca*-period is indentical with the Riss-Würm interglacial period. The fauna which was much richer than that of the upper arid period and the much milder and humider climate reconstructed on the basis of the fauna prove the interglacial time. On the intervalle of the *Mollusca*-period stratigraphically two parts may be distinguished: till 12,2 m it consists of humus-containing loess and below running sand. This running sand continues below the border of the *Mollusca*-period till 18,6 m. The aquatic fauna occurs in it continuously although only in small number (subperiod III./1) while further down in the loess (subperiod III./2) the aquatic organisms are lacking. Accordingly, the stratigraphical prolongation of the interglacial period downwards with the running sand is proved by the fauna too. The detailed analysis of the middle arid (III.) *Mollusca*-period, however, is the task of the following part of this series of publication.

According to MIHÁLTZ the running sand was transported by westerly winds from the bed of the Danube to this area. For the time of the origin of this running sand he supposes a climate which was milder and humider than that of the period of the origin of the loess but colder than the present climate. This means, that the inland ice-cover was sufficiently thin for permitting the activity of the westerly winds but at the same time this ice-cover hindered the development of climate as mild as that of today. The lower border of the upper humid *Mollusca*-period is not indicated by the sediments, the running sand pass through the subperiods II./4 and II./3 and ends with the lowest sample of the subperiod II./1. The border of the fauna at the end of the subperiod II./3 cor-

responds to the change of the climate-type, while the border of the running sand 20 cm above corresponds to the cease of the westerly winds. Above the border of the running sand the dominantly easterly winds are proved also by the formation of the loess. The direction of the winds was changed appearently by the thickening of the inland ice-cover. The process of the thickening of the inland ice-cover was the result of the climate-changes at the border of the subperiods II./3 and II./2 and it took place in the time when the lowest sample of the subperiod II./2 was formed (i. e. in the time of the formation of the uppermost sample of running sand.) The fauna of this sample is rich after all, but it is considerably poorer than the fauna of the neighbouring samples (especially in the sample below). The poor fauna too proves the worsening of the climate resulting from the thickening of the inland ice-cover. In the stratigraphically homogenous running sand the analysis of the fauna demonstrated four different climates and all of these climates were colder than that of today. The constant presence of the aquatic fauna in the running sand indicates the dominancy of the humidity transporting by westerly winds.

The humŭs containing loess was found between 12,2 and 10,8 m. Subperiods II./2 (except its lowest sample), II./1 and the lowest sample of the subperiod I./8 belong to here. The loess indicates a cold and arid continental climate and the dominancy of easterly winds while the presence of humus indicates a rich vegetation and a mild and humid climate necessary for the developing of such a rich vegetation. From these two follows a relatively mild period of loess formation whith a cold resistant vegetation: steppe with groves. All these corresponds the natural condition which were turned out from the detailed analysis of the fauna. The subperiod II./2 had a milder and humider, while subperiod II./1 had an arider, colder and more tundra-like character. On the basis of its fauna, among others on the basis of the lacking aquatic fauna, the lowest sample of the subperiod I./8 was placed already into the upper arid *Mollusca*-period. According to author's opinion the humus was formed here mostly from the vegetation in the milder and humider climate.

After all, MIHÁLTZ's conception on the process of sediment formation is in all confirmed by the fauna and the fauna corresponds also to the chronological denomination of the sediments. The analysis of the fauna brought new knowledges in the microstratigraphy and made possible a further division of the sediments too.

2. The astronomical chronology. In this chapter author compares the results obtained from the analysis of the fauna with the climate-curve of MILANKOVICH and BACSÁK, as in the case of the upper arid period. In the upper arid period the following of the climate-curve was only possible with the assumption that the Würm 2 and Würm 3 formed an united glacial period (kryon). The lower border of the kryon is indicated by the increase of the fauna, the permanent appearence of the aquatic fauna and the appearence of the first humus-containing zone. If so, the upper humid period is the sediment of the Würm 1 Würm 2 interstadial period and not that of the Riss — Würm interglacial period. The interglacial period Würm 1 is the sediment of the first loess (subperiod III./2) of the middle arid *Mollusca*-period. Advancing upwards on the climate-curve follow the climate changes described below.

Subarctic climate type. It was a duration of 10 400 years. In the profil corresponds to this period the part of the running sand layer located below

the upper humid period already mentioned above. In the fauna the subperiod II./1 corresponds to this climate-type. The average summers of this climate-type were only slightly effective against the chilling effect of the inland ice-cover. They melted, however, this ice-cover in such a degree that the westerly winds could deposit running sand. The cold winters of the climate type together with the chilling effect of the inland ice-cover were very unfavourable for the fauna. The very poor but constant occurring aquatic fauna indicates a tundra-like humidity as against the arid loess of the Würm 1 glacial period. The also very poor terrestric fauna corresponds not no the upper humid period but the middle arid period.

Antiglacial climate-type. It lasted 500 years; in the fauna the subperiod II./4. The warm summers of this climate-type limited the chilling effect of the inland ice and accelerated its melting. The winters too became milder, they were only average winters and the inland ice became thinner too. The vegetation became richer, it was a steppe-like one. The vegetation and fauna were favourably influenced by the presence the mostly from the melting-water feeded standing water. These favourable changes are shown from the considerable increase of the fauna. The short duration of the period corresponds to the short duration of the antiglacial period.

Subtropic (oceanic) climate-type. Its duration was 11 500 years; in the fauna the subperiod II./3. On the climate-curve from the four succeeding periods this was the most favourable from the point of view of the fauna with its averagely mild winters. Correspondingly, the fauna increased very considerably, it is here the richest. BACSÁK supposes a considerable diminishing of the inland ice-cover and a strenghtening of the vegetation. The rich fauna argues in the favour of the diminishing of the inland ice. A climate which was colder than that of today proves on every side the analysis of the fauna, and at the same time disproves the entire disappearence of the inland ice. The lower, relatively poor samples of the subperiod may indicate a thicker inland ice, the much richer upper samples a thinner inland ice. The formation of the sediment indicates no formation of forests, the formation of running sand continued further. The analysis of the fauna, however, indicated a formation of forests. The vegetation and the fauna were also here favourably influenced by the presence of standing water. The presence of standing water and its occasionally considerable increase is an other prove of the relatively mild oceanic climate-type.

Antiglacial climate type. It lasted 7 500 years; in the fauna the subperiod II./2 corresponds to it. From the point of view of the fauna this climate type with its warm summers and normal winters was more unfavourable, its beginning is proved already by the considerable decrease of the fauna. On the lower part of the subperiod the continental character was more expressed, the inland ice-cover chilled here the summers. According to BACSÁK the inland ice-cover became not so thick as thick it was yet in the time of the antiglacial period of 500 years. Accordingly, the fauna is here much richer than in the subperiod II./4. Further on, the gradual decrease of the aquatic and hygrophilic fauna and the considerable increase of the thermophilic fauna are the evidence of an after all warm and arid climate. Increase of the number of thermophilic organisms proves the vigourous melting of the inland ice. According to BACSÁK the inland ice entirely disapperaed to the end of the

antiglacial period. On the basis of the climate of the climatecurve the presence of a cold-steppe vegetation may be supposed. To this corresponds the formation of loess too. A vegetation, which was poorer than that of the former climate-type is proved by the fauna too, but on the basis of the fauna a steppe with groves may be supposed. Presence of groves is the probable consequence of the presence of standing water too. The appearence of humus on the stratigraphical profil may be attributed to the relatively rich littoral vegetation too.

Subarctics climate-type. Its duration is 3 000 years; in the fauna the subperiod II./1. The arid, continental climate, which is unfavourable for the fauna, here continued. The warm irradiation of the summers considerably decreased. The long and cold winters produced tundra-like conditions which infavourably influenced the fauna. On the basis of these it is natural, that the fauna is much poorer than that of the former subperiod. According to BACSÁK during this climate-type no inland ice-cover existed. Indeed, the fauna is much richer than at the time of the glacial subarctic oscillation of the upper humid period and at the time of the glacial subarctic oscillation of the upper arid period. This fact proves the correctness of BACSÁK's idea. Finally it must be mentioned, that inside the upper humid period the extent of the single subperiods and the duration of the corresponding climate-type of the climate curve show the same sequence.

After all on the basis of the analysis of the fauna of the upper humid period and on the basis of the subperiods of this fauna the astronomical climate-curve of MILANKOVICH and BACSÁK may be followed with success. With the aid of the fauna it succeeded the exact delimitation of the theoretical climate-types in the sediments too. The theoretical mounts of the climate-curve were filled up with concrete contents by the analysis of the fauna.

(To be continued.)

II. or the upper humid period of the boring of Felsőszentiván

Astronomical chronologie		Würm$_1$ — Würm$_2$ interstadial													
		Subarctic			Antiglacial			Subtropical						Anti-glacial	
Stratigraphical chronologie		Riss — Würm interglacial													
Mollusca subperiods		II/1			II/2			II/3						II/4	
Stratigraphical profil		Humus containing loess						Running sand							
Species	Depth. m.	11,0—11,2	11,2—11,4	11,4—11,6	11,6—11,8	11,8—12,0	12,0—12,2	12,2—12,4	12,4—12,6	12,6—12,8	12,8—13,1	13,1—13,4	13,4—13,7	13,7—14,0	14,0—14,3	14,3—14,5
Viviparus viviparus L.										1			1			
Valvata cristata O. F. Müll.		2				1	20	12	87	239	58	18	61	21	3	4
Valvata pulchella Stud.		1	4	17	1		14	25	147	462	109	32	92	20	2	2
Valvata piscinalis O. F. Müll.										4			3			
Bithynia tentaculata L.								1								
Bithynia leachi Shepp.							1	3	17	48	8	3	8	4		
Stagnicola palustris O. F. Müll.									7	19	9	3	5			3
Galba truncatula O. F. Müll.		3	2	2	5	15	41	56	350	1 085	264	64	242	55	7	8
Physa fontinalis L.							2					1				
Aplexa hypnorum L.							3	2	15	52	12	1	10	2		
Planorbis corneus L. iuv.							3	2	11	4		7	1	6		1
Anisus planorbis L.		1	1	1	2	6	18	30	83	292	87	25	77	12	2	4
Anisus carinatus O. F. Müll.								1	4					1		
Anisus vortex L.							1									
Anisus septemgyratus E. A. Bielz						2	6	1		5	2	2	2	1		
Anisus leucostoma Millet			6	9	45	88	174	101	511	49	11	7	31	7		
Anisus spirorbis L.		4	11	5	5	23	92	78	658	3 442	905	187	956	257	35	42
Bathyomphalus contortus L.									1		2					
Gyraulus albus O. F. Müll.										1						
Gyraulus laevis Alder					2	3	9	4	29	35	7	4	14	2	1	1
Gyraulus crista L.									1							
Gyraulus crista var. *nautileus* L.									3	11	3		3	1		
Segmentina nitida O. F. Müll.							1		3	5			1			
Pisidium cinereum Alder		1			8	3	27	8	101	238	114	33	54	13	3	6
Pisidium personatum Malm									2	9			3			
Pisidium obtusale C. Pfeiffer					2	1		6	5	14			3			2
Pisidium pulchellum Jenyns									1							
Pisidium mitidum Jenyns									1							
Aquatic species altogether		12	24	34	70	142	412	330	2 037	6 015	1 591	387	1 567	402	53	73
Carychium minimum O. F. Müll.		6	15	6	37	78	321	164	530	2 031	429	174	744	243	24	35
Succinea oblonga Drap.		160	76	45	397	721	1 060	625	2 816	7 409	2 110	532	1 278	302	43	90
Amphibiotic species altogether		166	91	51	434	799	1 381	789	3 346	9 440	2 539	706	2 022	545	67	125
Cochlicopa lubrica O. F. Müll.		32	14	20	77	49	86	52	156	345	113	57	64	20	4	12
Vertigo pygmaea Drap.		86	74	54	266	298	344	204	1 169	2 285	512	178	1 190	372	43	36
Vertigo antivertigo Drap.							7	10	136	196	23	15	63	13	4	2
Vertigo angustior Jeffreys			7	3	46	36	45	25	138	203	42	19	120	32	3	8
Pupilla muscorum L.		155	100	51	207	373	442	103	359	262	41	31	119	49	4	5
Vallonia pulchella O. F. Müll.		51	40		297	275	771	182	732	1 604	228	151	202	223	43	26
Vallonia enniensis Gredler		17	20	17	220	209	140	188	1 109	2 968	821	138	1 066	152	29	27
Vallonia costata O. F. Müll.		62	39	75	118	103	63	23	95	73	68	9	20	11	3	
Punctum pygmaeum Drap.		1	2	6	13	16	10	5	15	13	4	2	3	1		1
Vitrea crystallina O. F. Müll.		12	5		13	2	10	2	6	3	1		2			
Euconulus trochiformis Mont.					3	1	6	12	152	348	118	41	105	18	3	2
Deroceras agreste L.		15	9	8	31	38	33	24	145	357	94	20	33	5	2	6
Trichia hispida L.		67	30	21	56	69	117	57	260	110	51	13	32	12	6	2
Hygrophil ubiquist species altogether		498	340	255	1 347	1 469	2 074	887	4 472	8 767	2 116	674	3 019	908	144	127
Pupilla sterri Voith		3							9	12	8		35			
Clausilia dubia Drap.					1											
Goniodiscus ruderatus Studer		2			4	1	5	1	3	8	2	1	1			
Perpolita hammonis Ström		28	20	7	32	32	47	16	106	197	45	7	47	6	1	2
Fruticicola fruticum O. F. Müll.		3	8	2	4	3	3	7	4	4			10			
Perforatella bidens Chemn.		1			21	4	24	4	15	18	7	3	9			
Arianta arbustorum L.		2			9	3	3	13	18	34	35	8	2	9	2	2
Inhabitant of the groves altogether		39	28	9	71	43	82	41	155	273	97	19	104	15	3	4
Abida frumentum Drap.		22	21	18	26	100	3		10	12	1		1	2		
Imparietula tridens O. F. Müll.		44	30	41	15	33	14	14	25	51	21	9	9	9	2	3
Helicella hungarica Soós et h. Wagner		2			4	3		1	5	1		3	1			
Thermophilic species altogether		68	51	59	45	136	17	15	40	64	22	12	11	11	2	3
Vallonia tenuilabris Al. Braun									3							
Mollusca exemplars altogether		783	534	408	1 967	2 589	3 966	2 062	10 053	24 559	6 365	1 798	6 723	1881	269	332

DAS LEBEN DER TISZA
XXV. DIE QUANTITATIVEN, BZW. SAPROBIOLOGISCHEN VERHÄLTNISSE DES PHYTOPLANKTONS IM SZOLNOKER FLUSSABSCHNITT

von

G. UHERKOVICH

Biologische Station für Tiszaforschung der Universität Szeged, Ungarn

Die Wirkung der verschiedenen Verunreinigungen auf die Lebewelt unserer grösseren Flüsse zu erforschen, ist sowohl von allgemeinen potamolimnologischen, als auch von praktischen Gesichtspunkten der Saprobiologie gleichermassen wichtig.

Bei der Untersuchung der Tisza, des längsten — und hinsichtlich der Wasserversorgung der Ungarischen Tiefebene (Alföld) wichtigsten — Nebenflusses der Duna (Donau) ist vor allem zu beachten, dass dieser Fluss an folgenden Orten Verunreinigungen erfährt: 1. = Einmündung der Bodrog (die Bodrog wird auf tschechoslowakischem Boden mit industriellen Abwässern belastet), 2. = Einmündung des Sajó (der Sajó nimmt in der Tschechoslowakei und auf ungarischem Gebiet industrielle und Haushaltsabwässer auf), 3. = Tiszapalkonya (Abwasseraufnahme aus den immer grösser werdenden chemischen Betrieben usw.), 4. = Szolnok (industrielle Abwässer verschiedener Betriebe, bedeutende Mengen Haushaltsabwasser, Einmündung der Zagyva, die sicht im Bereich Hatvan mit industriellem Abwasser belastet und bei Szolnok die Abwässer des Krankenhauses aufnimmt), 5. = Szeged (ausgiebigere Haushalts- und relativ geringgradigere industrielle Abwasserbelastung).

Von den durch Verunreinigungen stärker gefährdeten Flussbettstrecken scheint die eingehendere Untersuchung *bei Szolnok* am wichtigsten und dringendsten, und zwar auf Grund der folgenden Überlegungen. Jede wesentlichere Abwasserbelastung der Tisza auf ungarischem Boden erfolgt oberhalb von Szolnok und bei Szolnok selbst. Hinsichtlich der oberhalb von Szolnok stattfindenden Wasserentnahme zu Bodenberieselungszwecken und zur Trinkwassergewinnung [Szolnok deckt seit über 30 Jahren seinen Trinkwasserbedarf aus dem Fluss] ist das limnologisch-saprobiologische Gesamtbild des bei Szolnok eintreffenden Tiszawassers keineswegs indifferent, desgleichen auch die Frage nicht, wie gross, bzw. welcher Art der Einfluss der weiteren Abwasserbelastung bei Szolnok auf die Lebewelt des Flusses ist und wie es um das Selbstreinigungsvermögen des Flusses unterhalb von Szolnok steht. Die Klärung dieser Fragen ist nicht nur gegenwärtig, sondern auch für die Zukunft wichtig, denn einerseits muss, trotz aller Vorsichtsmassnahmen, mit einer gewissen weiteren Steigerung der Abwasserbelastung bei Tiszapalkonya und Szolnok gerechnet werden und andererseits muss auch den speziellen Fragen

der Qualität des in dem oberhalb von Szolnok zu errichtenden zweiten Stauwerk zur Speicherung gelangenden Wassers Rechnung getragen werden.

Es versteht sich von selbst, dass eine Antwort auf die skizzierten Fragen nur durch wiederholte, zu verschiedenen Jahreszeiten und bei verschiedenen Flusszuständen vorgenommene Untersuchungen zu erhalten ist.

Ich muss betonen, dass ich nicht beabsichtige, die ausschliesslich wasserqualifizierende Gesichtspunkte berücksichtigende Arbeit des praktischen Saprobiologen zu vollziehen, aber erreichen möchte, dass meine — nach allgemeinen potamolimnologischen Gesichtspunkten durchgeführten — Arbeiten auch für die praktische Saprobiologie von Nutzen seien. Ich war deshalb bestrebt, ein *allgemeingültigeres potamolimnologische Bild* von der mikroskopischen Pflanzenwelt zu entwerfen, welches auch die *Ansprüche der Saprobiologie* berücksichtigt.

Die eingehende Untersuchung des Flussbettes ober- und unterhalb von Szolnok haben wir im Jahre 1960 im Rahmen des Forschungsprogrammes der Szegeder Tiszaforschungsstation in Angriff genommen. Einerseits haben wir von Szolnok aufwärts bis zu dem beim 60 km weit liegenden Tiszabura alle 20 km, und abwärts bis zu dem beim 87 km weit sich ausbreitenden Csongrád alle 20—25 km Proben entnommen und andererseits zur Erforschung des unmittelbaren Einflusses der Abwässer von Szolnok Proben von den unterhalb der fünf bedeutenderen Abwasserkanäle befindlichen Stellen des Flusses eingeholt. Endlich wurden — sozusagen um die Vorteile der beiden verschiedenen Probenentnahmen zu vereinigen — Proben oberhalb der Stadt gesammelt, wo die Wasserentnahme für das Wasserwerk stattfindet, sowie unterhalb der Stadt bei Tiszavárkony dort, wo die Vermischung des Wassers vollkommen ist und partielle Selbstreinigung eintritt. Über die Ergebnisse der beiden ersten Probenentnahmen [1960—61] bezüglich des Phytoplanktons habe ich bereits berichtet [UHERKOVICH, 1962], so dass ich hier nicht auf sie einzugehen brauche. In der vorliegenden Studie möchte ich die Ergebnisse der Aufarbeitung der 1962 ober- und unterhalb von Szolnok eingeholten Flusswasserproben bekanntgeben. Die Materialsammlung fand während der Monate Februar bis September statt, d. h. zu einer Zeit, wo die Zuckerfabrikation ruhte. Hauptziel der Untersuchungen war die Aufdeckung der Verhältnisse, die während der verschiedenen Jahreszeiten *ausserhalb der Zuckerproduktionskampagne* — aber bei Aufnahme der übrigen industriellen und Haushaltsabwässer im Flussabschnitt bei Szolnok zur Entwicklung gelangen. [Frühere Untersuchungen hatten nämlich gezeigt, dass während der Zuckerherstellungskampagne die Verunreinigung der Tisza bei Szolnok — und auch der hier einmündenden Zagyva — anderer Art ist als während der übrigen Periode.]

Die zur *quantitativen* Aufarbeitung des Phytoplanktons geschöpften Proben wurden nach der UTERMÖHLschen Sedimentationsmethode [UTERMÖHL, 1931, 1958] mit Hilfe des mir vom Biologischen Forschungsinstitut Tihany zur Verfügung gestellten umgekehrten Planktonmikroskops [Zeiss-Oberkochen] untersucht. Die Resultate sind in Individuen/l-Werten angegeben. Die gleichzeitig eingeholten Planktonproben [Planktonnetz 25] dienten zur Ergänzung der *qualitativen* Daten des Phytoplanktons. Hier ist hervorzuheben, dass die mit der UTERMÖHLschen Methode erhaltenen qualitativen Phytoplankton-

Ergebnisse für Organismengruppen aller Grössenordnungen — d. h. auch sogar hinsichtlich des Nannoplanktons — als vollkommen exakt zu betrachten sind.

Die ausführlichen Ergebnisse der qualitativen und quantitativen Analyse des im Laufe des Jahres 1962 zu drei verschiedenen Zeitpunkten *bei Szolnok entnommenen Phytoplanktons* veranschaulicht die beiliegende Tabelle. Sie gibt — unter Berücksichtigung der oberhalb und unterhalb von Szolnok [Tiszavárkony bzw. Tiszaug] angestellten Sammlungen — Auskunft über das Vorkommensverhältnis von 153 Taxonen. Wo Gewähr für entsprechende Sicherheit bestand, habe ich auch angegeben, welchem Typ von Saprobionten der betreffende Mikroorganismus angehört.

Bei jenen Organismen, die nur aus dem Filtrat der Netzplanktonproben grösserer Wassermengen zum Vorschein kamen, d. h. zu dem fraglichen Zeitpunkt im Flusse nur in geringerer Zahl vorhanden waren, ist in der entsprechenden Rubrik der Tabelle ein + eingetragen, während bei den übrigen auch die bei der quantitativen Analyse erhaltenen Individuum/l-Werte angegeben sind. Bei den kleisten Mitgliedern des Nannoplanktons besteht natürlich die Möglichkeit, dass sie fallweise in den geschöpften Wasserproben in bestimmter Menge nachweisbar waren, in den Netzproben aber nicht gesichtet wurden.

Die wichtigeren Ergebnisse der einzelnen Sammlungen lassen sich folgendermassen zusammenfassen:

Die *Sammlung vom 27. Februar 1962* wünschte den typischen *Winterend-Aspekt*, nach Abtreiben der Eisdecke, zu erfassen. Die Wassertemperatur betrug 0,2 C°. Das Phytoplankton der oberhalb von Szolnok entnommenen Proben mit seinen 12,400 Gesamtindividuen pro Liter gestaltete sich folgendermassen:

Synedra ulna	21,0%	o—β—m
Diatoma vulgare	21,0%	o—β—m
andere *Bacillarioph.*	46,6%	
Chlamydomonas spp.	8,2%	β—α—m
weitere Algen	3,2%	

Unterhalb von Szolnok waren zur gleichen Zeit [bei Tiszavárkony] nur 3040 Gesamtindividuen/l nachweisbar, deren Zusammensetzung folgende Charakterzüge aufwies:

Synedra ulna	49,6%	o—β—m
Diatoma vulgare	5,3%	o—β—m
andere *Bacillarioph.*	13,7%	
Chlamydomonas spp.	15,9%	β—α—m
Cladothrix dichotoma	10,5%	p—α—m
weitere Algen	5,0%	

Dieser Winterend-Aspekt des Phytoplanktons war überaus ärmlich und von niedriger Individuenzahl. Eine gewisse Dominanz erreichte *Synedra ulna.* Oberhalb von Szolnok waren insgesamt 30, und unterhalb von Szolnok 39 Taxone nachweisbar. In der mässigen Erhöhung der Artenzahl dürften die von der Zagyva eingetragenen Organismen eine Rolle gespielt haben. Die Verschlechterung der Wasserqualität unterhalb von Szolnok zeigt das Er-

scheinen der *Cladothrix dichotoma* in relativ grossen Mengen, sowie die Vermehrung der relativen *Chlamydomonas*populationen. Die Gesamtindividuen/l-Werte im Bereich von Szolnok waren jetzt auf 1/4 gesunken. Dies, sowie die weitere Verschlechterung der Wasserqualität dürfte als Folge der Verunreinigung mit industriellen Abwässern zu betrachten sein. Oberhalb von Szolnok hat der Flussabschnitt jetzt — auf Grund des Gesamtbildes — β-mesosaproben, und die unterhalb von Szolnok gelegene Strecke einen schlechteren, dem α-mesosaproben nahekommenden α—β-mesosaproben Charakter. Hier ist aller Wahrschenlichkeit nach davon die Rede, dass das infolge der ungünstigen ökologischen Verhältnisse dieser Jahreszeit zur Entwicklung gelangte, sehr ärmliche Phytoplankton auf die industriellen Verunreinigungen empfindlich reagierte.

In der *Sammlung vom 6. Juni 1962* sollte der auf die durch anhaltend hohen Wasserstand charakterisierte Frühjahrsperiode folgende — bei wechselndem Wasserstand entwickelte — *Sommeranfangs-Aspekt* erfasst werden. Die Wassertemperatur betrug 16,7 C°. Das Phytoplankton gestaltete sich bereits weit reichhaltiger als im Winter, doch weisen die sich auf einige zehntausend beziehenden Gesamtindividuen/l-Werte — gemäss dem wechselnden Wasserstande und der infolgedessen wechselnden Durchsichtigkeit des Wassers, sowie der wechselnden, im allgemeinen aber noch niedrigen Wassertemperatur — in dieser Periode noch ziemlich grosse Schwankungen auf. Am Tage der Sammlung enthielt das Phytoplankton *oberhalb von Szolnok* 25,000 Gesamtindividuen pro Liter mit folgender Zusammensetzung:

Synedra ulna	24%	o—β—m
Ceratoneis arcus	14%	o
Diatoma vulgare	10%	o—β—m
Nitzschia acicularis	4%	β—α—m
andere *Bacillarioph.*	38%	
Chlamydomonas spp.	6%	β—α—m
weitere Algen	4%	

Unterhalb von Szolnok [Tiszavárkony] resultierten zur gleichen Zeit Gesamtindividuen/l-Werte von 44,500 mit folgenden Charakterzügen:

Synedra ulna	20,3%	o—β—m
Ceratoneis arcus	15,7%	o
Diatoma vulgare	9,0%	o—β—m
Nitzschia acicularis	7,9%	β—α—m
andere *Bacillarioph.*	34,2%	
Chlamydomonas spp.	6,9%	β—α—m
weitere Algen	6,0%	

Oberhalb von Szolnok ergab sich eine Taxon-Zahl von 40 und unterhalb von Szolnok von 43. Der Anstieg der Taxon-Ziffer und der Gesamtindividuen/l-Werte ist auf die Beimengung des weitaus reicher bevölkerten Zagyva-Planktons zurückzuführen. Das Wasser der Tisza kann zu dieser Zeit sowohl ober- als auch unterhalb von Szolnok auf Grund seines Gesamtbildes als β-mesosaprob angesprochen werden.

Die *Sammlung vom 5.—6. September 1962 [Sommerende-Herbstanfang]* stellt das auf die Wirkung das anhaltend niedrigen Wasserstandes [wenig

schwebende Mineralstoffe, grössere Durchsichtigkeit des Wassers und somit eine dickere photosynthetisch-aktive Wasserschicht] und der dauernd höheren Wassertemperatur entlang des ganzen Flusslaufes zustandekommende, das Produktionsmaximum anzeigende, artenreichste Phytoplankton dar. Die Wassertemperatur betrug zur Zeit der Sammlung 21 C°. *Oberhalb von Szolnok* ergibt jetzt die quantitative Analyse 526,250 Gesamtindividuen pro Liter. Aus der Zusammensetzung des Phytoplanktons sind folgende Charakteristika hervorzuheben:

Cyclotella spp.	23,50%	
Synedra actinastroides	3,71%	β–α–m
Melosira granulata var. *angustissima*	2,85%	β–α–m
M. granulata var. *angustissima* f. *spiralis*	2,38%	β–α–m
Chaetoceros muelleri forma	6,20%	
Nitzschia acicularis	2,20%	β–α–m
andere *Bacillarioph.*	14,01%	
Chlamydomonas spp.	8,79%	β–α–m
Coelastrum cambricum	4,28%	
Scenedesmus spp.	11,10%	β–α–m, β–m
weitere Chlorophyten	15,44%	
weitere Algen	9,99%	

Unterhalb von Szolnok [diese Sammlung stammt ausnahmsweise nicht von Tiszavárkony, sondern von Tiszaug, d. h. etwas weiter abwärts] ergab die quantitative Analyse zu dieser Zeit 788,750 Gesamtindividuen/l; die charakteristischen Züge der Phytoplanktonzusammensetzung waren folgende:

Cyclotella spp.	12,84%	
Synedra actinastroides	5,07%	β–α–m
Melosira granulata var. *angustissima*	4,44%	β–α–m
M. granulata var. *angustissima* f. *spiralis*	15,53%	β–α–m
Chaetoceros muelleri forma	5,86%	
Nitzschia acicularis	1,43%	β–α–m
andere *Bacillarioph.*	5,07%	
Clamydomonas spp.	2,54%	β–α–m
Coelastrum cambricum	10,62%	
Scenedesmus spp.	12,84%	β–α–m, β–m
weitere Chlorophyten	20,59%	
weitere Algen	3,17%	

Eine auffallende Abweichung zwischen Winterend- und Sommeranfang-Aspekt ist, dass jetzt in dem an Populationen reicheren und wechselvoller zusammengesetzten Phytoplankton die Grünalgen — und innerhalb dieser besonders die *Chlorococcales*-Arten — eine fast gleichrangige Rolle einnehmen wie die Kieselalgen. Von den Kieselalgen ist *Synedra ulna* quantitativ vollkommen in den Hintergrund gedrängt, während *Cyclotella*-Arten Dominanz erreichen und die Massenproduktion von *Melosira granulata* var. *angustissima*, sowie deren f. *spiralis* einsetzt und im Laufe des September immer weiter fortschreitend am Flusslauf abwärts stetig zunimmt. Beachtenswert ist jetzt noch die hochgradige Vermehrung der *Chaetoceros muelleri*-Individuenzahl und von den *Chlorococcales* der *Scenedesmus*-Arten und des *Coelastrum cambricum*.

Die Zusammensetzung des Phytoplanktons zeugt von der ständigen Eutrophierung des Wassers. Das Wasser ist — bereits auch schon oberhalb von Szolnok — entschieden β—α-mesosaproben Charakters. Seine reiche Lebewelt vermag die infolge des niedrigen Wasserstandes sich stärker bemerkbar machende Abwasserbelastung zwar noch zu verarbeiten und auch das Selbstreinigungsvermögen des Flusses ist noch befriedigend, doch macht gerade die beträchtliche Annäherung an den α-mesosaproben Zustand darauf aufmerksam, dass im Falle sehr niedrigen Wasserstandes eine grössere Abwasserbelastung als die gegenwärtige einen sehr plötzlichen Umschlag in ein wesentlich ungünstigeres Sabprobitätsverhältnis herbeiführen kann. [Hier ist zu bemerken, dass flussabwärts gleichzeitig ein stetiges Anwachsen der Phytoplanktonpopulationen bis zu 1,500,000—2,000,000 Gesamtindividuen/l zu verzeichnen ist.].

Taxonomisch gesehen ist das Vorkommen der *Pleodrina californica* SHAW. (s. Mikrophotogramm) und einer neuen *Lambertia*-Variante — *Lambertia ocellata* KORSCHIK. var. *maxima* UHERK. — interessant, die sich von der Art und auch vom Typ durch ihre grösseren Zellmasse unterscheidet [Art: 45×5 μ, Variante: 120—160×10—13 μ; s. Mikrophoto und Zeichnung].

Bei der *zusammenfassenden Darstellung* der in der vorliegenden Studie aufgearbeiteten Forschungsergebnisse ist folgendes hervorzuheben: 1. Die Planktonproduktion hat ihr Minimum zu Ende des Winters und ihr Maximum zu Ende des Sommers bzw. Anfang des Herbstes erreicht. 2. Zwischen den Gesamtindividuen/l-Werten der minimalen und der maximalen Planktonproduktion ergeben sich aussergewöhnliche grosse [im vorliegenden konkreten Falle 260-fache] Unterschiede. 3. Vom Winter bis zum Hochsommer beherrschen die Kieselalgen quantitativ das Phytoplankton, während zu Ende des Sommers, bzw. zu Beginn des Herbstes eine gemeinsame Dominanz von Kiesel- und Grünalgen zur Entwicklung gelangt. 4. Der untersuchte Flussabschnitt hat β- bzw. β—α-mesosaproben Charakter; auf die Einwirkung der hier einströmenden Abwässer ist eine gewisses Nachlassen des Saprobitätsgrades des Wassers festzustellen, doch verfügt der Fluss hier noch über eine hinreichende Selbstreinigungsfähigkeit. 5. Mehrere Zeichen deuten darauf hin, dass auf den Einfluss grösserer Abwasserbelastungen als die gegenwärtige — besonders zur Zeit der durch einen niedrigen Wasserstand charakterisierten Perioden — an dieser und den anschliessenden Flusstrecken weitaus schlechtere Saprobitätsverhältnisse zur Entwicklung gelangen können.

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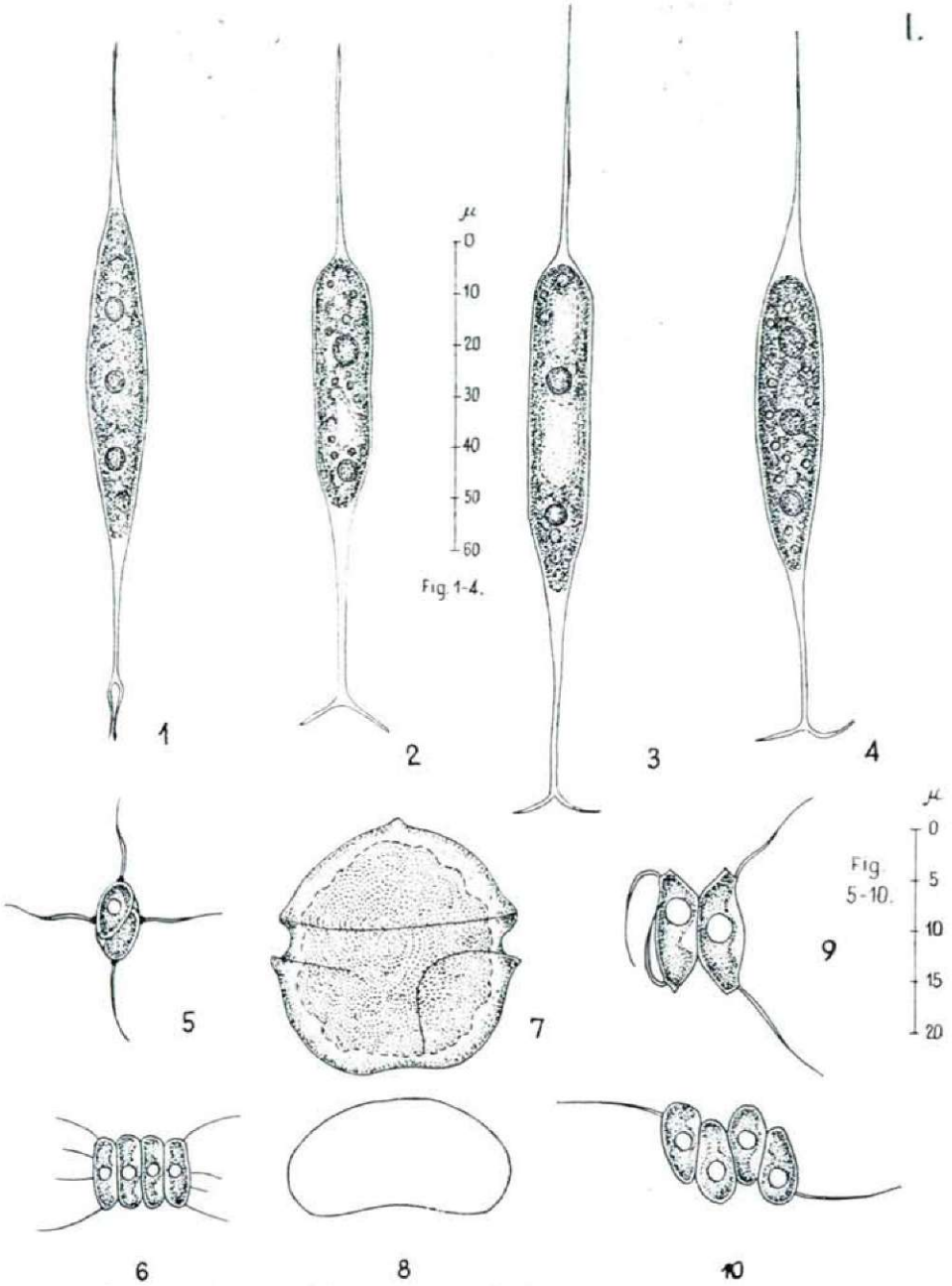
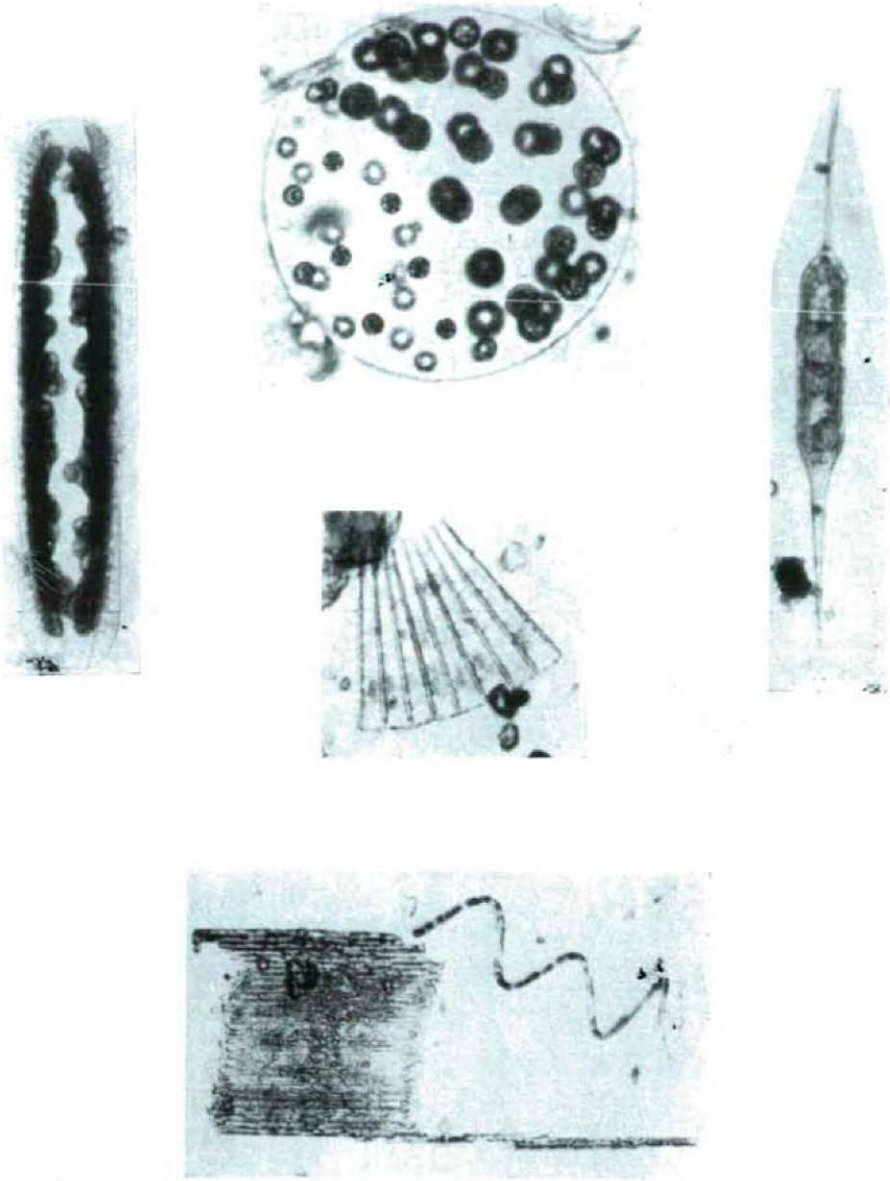


1—4. Lambertia ocellata Korschik var. maxima Uherkov.
5. Lagerheimia wratislaviensis Schroed.
6. Scenedesmus spinosus Chod. var. tenuispina (Chod.) Uherkov.
7—8. Glenodinium sp.
9. Scenedesmus opoliensis P. Richt.
10. Scenedesmus intermedius Chod. var. bicaudatus Hortob.



1. Surirella biseriata Bréb.
2. Pleodorina californica Shaw.
3. Meridion circulare Agh.
4. Lambertia ocellata Korschik. var. maxima Uherkov.
5. Bacillaria paradoxa Gmelin und
   Melosira granulata (Ehrbg.) Ralfs var. angustissima Müll.
   f. spiralis Müll.

Übersicht über das Potamophytoplankton der Tisza im Szolnoker Flußabschnitt (Februar—September 1962)

		27. 2. 1962.				6. 6. 1962.				5—6. 9. 1962.			
		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok	
		ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe
		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
	SCHIZOMYCOPHYTA-MYCOPHYTA												
1.	*Cladothrix dichotoma* COHN p—α—m		+	320	+								
2.	*Sphaerotilus natans* KÜTZ. p				+								
3.	*Zoogloea ramigera* ITZIGSOHN p						+						
	CYANOPHYTA												
4.	*Lyngbya aerugino-coerulea* [KÜTZ.] GOM.				+								
5.	*Merismopedia punctata* MEYEN α—β—m												
6.	*Microcystis flos-aquae* [WITTR.] KIRCHN. β—m										+		+
7.	*Nostoc coeruleum* LYNGB.				+								+
8.	*Oscillatoria curviceps* AGH.		+										
9.	*Oscillatoria limosa* KÜTZ. β—m								+				
10.	*Oscillatoria simplicissima* GOM. β—m				+								
11.	*Oscillatoria tenuis* AGH. α—m		+				+					1 250	+
12.	*Phormidium corium* [AGH.] GOM. β—m		+		+								
	EUGLENOPHYTA												
13.	*Euglena acus* [O. F. M.] EHRBG. β—m						+	500	+		+		
14.	*Euglena proxima* DANG. β—m								+	7 500	+	1 250	+
15.	*Euglena* spp.										+		
16.	*Petalomonas* spp.					•				7 500	+		+
17.	*Strombomonas fluviatilis* [LEMM.] DEFL. β—α—m							500	+				
18.	*Strombomonas* sp.							500					
19.	*Trachelomona* spp.												

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
	PYRROPHYTA												
20.	*Glenodinium* sp.										+		
21.	*Ceratium hirundinella* [O. F. M.] Schrank f. *furcoides* (Schroed.) H.—P.										+		+
	CHLOROPHYTA												
	Chlorophyceae												
22.	*Actinastrum hantzschii* Lagerh. β—m				+				+	6 250	+	13 750	+
23.	*Ankistrodesmus acicularis* [A. Br.] Korschik. β—α—m								+	18 750	+	30 000	+
24.	*Ankistrodesmus angustus* Bern.									5 000	+	23 750	+
25.	*Ankistrodesmus braunii* [Naeg.] Brunnth.												
26.	*Ankistrodesmus falcatus* (Corda) Ralfs β—m				+						+		
27.	*Chlamydomonas reinhardii* Dang. β—α—m												+
28.	*Chlamydomonas* spp.	1 000	+	480	+	1 500	+	3 000	+	46 250	+	20 000	+
29.	*Coelastrum cambricum* Arch.									22 500	+	83 750	+
30.	*Coelastrum microporum* Naeg. β—m										+	1 250	+
31.	*Crucigenia apiculata* Schmidle β—m									1 250	+	3 700	+
32.	*Crucigenia tetrapedia* (Kirchn.) W. et G. S. West β—α—m										+	20 000	+
33.	*Dictyosphaerium ehrenbergianum* Naeg.										+		
34.	*Dictyosphaerium pulchellum* Wood				+		+			7 500	+	2 500	+
35.	*Eudorina charkowiensis* Pascher				+				+				
36.	*Eudorina elegans* Ehrbg. β—m		+				+		+		+		+
37.	*Gonium pectorale* Müll. β—m									1 250	+		+
38.	*Lambertia ocellata* Korschik. var. *maxima* Uherkovich									2 500	+		
39.	*Lagerheimia wratislaviensis* Schroed.									5 000	+	2 500	+
40.	*Micractinum bornhemiense* (Conr.) Korschik.										+		
41.	*Micractinium pusillum* Fres.									3 750	+	8 750	+
42.	*Microspora* sp.				+								
43.	*Oocystis borgei* Snow β—m									3 750	+	5 000	+
44.	*Pandorina morum* Bory β—m				+	500	+						
45.	*Pediastrum boryanum* (Turp.) Menegh. β—α—m						+				+		+

		27. 2. 1962.				6. 6. 1962.				5—6. 9. 1962.			
		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok	
		ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe	ind./l	Netz-probe
		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
46.	*Pediastrum duplex* MEYEN β—α—m										+		+
47.	*Pediastrum simplex* (MEYEN) LEMM. β—α—m												+
48.	*Pediastrum tetras* (EHRBG.) RALFS β—m									1 250	+	1 250	+
49.	*Pleodorina californica* SHAW												+
50.	*Scenedesmus acuminatus* (LAGERH.) CHOD. β—m					500	+			8 700	+	13 750	+
51.	*Scenedesmus acuminatus* var. *elongatus* G. M. SMITH										+		+
52.	*Scenedesmus acutus* MEYEN β—m												+
53.	*Scenedesmus bicaudatus* (HANSG.) CHOD.										+		
54.	*Scenedesmus ecornis* (RALFS) CHOD. β—m									6 000	+	5 000	+
55.	*Scenedesmus granulatus* W. et G. S. WEST									3 000	+	5 000	+
56.	*Scenedesmus intermedius* CHOD.									12 500	+	20 000	+
57.	*Scenedesmus intermedius* var. *bicaudatus* HORTOB.									500	+	23 750	+
58.	*Scenedesmus opoliensis* P. RICHT. β—m	200	+					500	+	8 750	+	5 000	+
59.	*Scenedesmus protuberans* FRITSCH									2 500	+	6 250	+
60.	*Scenedesmus quadricauda* (TURP.) BRÉB. β—α—m									8 000	+	10 000	+
61.	*Scenedesmus soói* HORTOB.							500	+			2 000	+
62.	*Scenedesmus spinosus* CHOD. var. *tenuispina* (CHOD.) UHERKOV.									4 000	+	5 000	+
63.	*Schroederia setigera* LEMM.											1 250	+
64.	*Selenastrum gracile* REINSCH									6 250	+	10 000	+
65.	*Siderocystis fusca* KORSCHIK.									2 500			
66.	*Sphaerocystis schroeteri* CHOD.												+
67.	*Stigeoclonium lubricum* KÜTZ.												
68.	*Tetraëdron minimum* (A. BR.) HANGS.						+			2 500		20 000	+
69.	*Tetrastrum staurogeniaeforme* (SCHROED.) LEMM.									1 250	+		+

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
70.	*Ulothrix tenerrima* KÜTZ.		+						+				
71.	*Ulothrix tenuissima* KÜTZ.		+		+								
	Conjugatophyceae												
72.	*Closterium lanceolatum* KÜTZ.										+		+
73.	*Closterium limneticum* LEMM. β—m								+				
74.	*Closterium parvulum* NAEG. β—m										+		
75.	*Closterium pseudolunula* BORGE								+				
76.	*Mougeotia* sp.												
77.	*Spirogyra* spp.						+		+				+
78.	*Staurastrum tetracerum* (KÜTZ.) RALFS										+		
	CHRYSOPHYTA *Chrysophyceae—* *Xanthophyceae*												
79.	*Dinobryon bavaricum* IMHOF										+		
80.	*Dinobryon divergens* IMHOF						+		+		+		+
81.	*Dinobryon sertularia* EHRBG. β—m						+		+				
82.	*Synura uvella* EHRBG. α—β—m						+		+		+		
83.	*Tribonema minus* G. S. WEST	200	+		+								
	Bacillariophyceae												
84.	*Amphora ovalis* KÜTZ. o—β—m				+								
85.	*Asterionella formosa* HASSAL o—β—m						+		+		+		+
86.	*Bacillaria paradoxa* GMELIN β—m										+		+
87.	*Caloneis amphisbena* (BORY) CLEVE β—m	600	+		+								+
88.	*Caloneis silicula* (EHRBG.) CLEVE var. *truncatula* GRUN.				+								
89.	*Campylodiscus noricus* EHRBG. var. *hibernica* (EHRBG.) GRUN.						+		+				
90.	*Ceratoneis arcus* KÜTZ. o	800	+			3 500	+	7 000	+	32 500	+	46 250	+
91.	*Chaetoceros muelleri* LEMM. forma												
92.	*Cocconeis pediculus* EHRBG. β—m				+						+		
93.	*Cyclotella chaetoceros* LEMM. forma												
94.	*Cyclotella ocellata* PANT.						+						
95.	*Cyclotella* spp.	200				500		2 000	+	121 250	+	101 250	+
96.	*Cymatopleura elliptica* (BRÉB.) W. SMITH o—β—m				+				+				

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		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok		oberhalb Szolnok		unterhalb Szolnok	
		ind./l	Netzprobe	ind./l	Netzprobe	ind./l	Netzprobe	ind./l	Netzprobe	ind./l	Netzprobe	ind./l	Netzprobe
		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
97.	*Cymatopleura solea* (Bréb.) W. Smith β—α—m								+	1 250	+	1 250	+
98.	*Cymatopleura solea* var. *regula* (Ehrbg.) Grun.										+		
99.	*Cymatopleura solea* var. *subconstricta* O. F. M. f. *minor* O. F. M.												+
100.	*Cymbella cymbiformis* (Kütz.) v. Heurck β—m			120	+								
101.	*Cymbella prostrata* (Berkeley) Cleve β—α—m	600			+								
102.	*Cymbella ventricosa* Kütz. β—α—m	400											
103.	*Diatoma vulgare* Bory o—β—m	2 600	+	120	+	2 500		4 000	+				
104.	*Diatoma vulgare* var. *brevis* Grun.		+										
105.	*Diatoma vulgare* var. *producta* Grun. β—α—m						+						
106.	*Fragilaria capucina* Desmaz. o—β—m		+						+				
107.	*Fragilaria construens* (Ehrbg.) Grun. o—β—m								+				
108.	*Fragilaria crotonensis* Kitton o—β—m				+		+		+				
109.	*Gomphonema olivaceum* (Lyngb.) Kütz. β—m										+		
110.	*Gomphonema* sp.					500		1 500					
111.	*Gyrosigma acuminatum* (Kütz.) Rabenh. o—β—m												+
112.	*Gyrosigma attenuatum* (Kütz.) Rabenh.	400	+		+								
113.	*Gyrosigma kützingii* (Grun.) Cleve				+								
114.	*Melosira granulata* (Ehrbg.) Ralfs var. *angustissima* Müll. β—α—m						+			15 000	+	35 000	+
115.	*Melosira granulata* var. *angustissima* f. *spiralis* Müll. β—α—m								+	12 500	+	122 500	+
116.	*Melosira varians* C. A. Agh. β—α—m	200	+		+					1 250	+		+

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
117.	*Meridion circulare* AGH. o					500	+						
118.	*Nabicula cryptocephala* KÜTZ.	200											
119.	*Navicula radiosa* KÜTZ. β—m	600											+
120.	*Navicula tuscula* (EHRBG.) GRUN.					1 500		500					+
121.	*Navicula viridula* KÜTZ. β—m					1 000	+	3 500	+	11 250	+	11 250	
122.	*Nitzschia acicularis* W. SMITH β—α—m				+								+
123.	*Nitzschia acuta* HANTZSCH β—α—m												
124.	*Nitzschia hantzschiana* RABENH. β—m		+										+
125.	*Nitzschia heufleriana* GRUN.												
126.	*Nitzschia linearis* W. SMITH o—β—m	200	+				+	1 000	+	3 750	+	3 750	+
127.	*Nitzschia longissima* (BRÉB.) RALFS var *closterium* (W. SMITH) v. HEURCK	200											+
128.	*Nitzschia lorenziana* GRUN. var. *subtilis* GRUN.	600									+		+
129.	*Nitzschia palea* (KÜTZ.) W. SMITH	200	+	120	+								
130.	*Nitzschia obtusa* W. SMITH. β—α—m	600			+		+	2 000	+	6 250	+		+
131.	*Nitzschia sigmoidea* (EHRBG.) W. SMITH β—α—m		+	120	+		+		+		+		
132.	*Nitzschia tryblionella* HANTZSCH var. *victoriae* GRUN.									2 500			+
133.	*Nitzschia vermicularis* (KÜTZ.) GRUN. α—m					500	+	500	+				+
134.	*Pinnularia viridis* (NITZSCH) EHRBG. β—m				+								
135.	*Pleurosigma elongatum* W. SMITH				+								
136.	*Stauroneis anceps* EHRBG. β—m										+	1 250	
137.	*Stauroneis parvula* GRUN.										+		+
138.	*Stauroneis phoenicentron* EHRBG. o—β—m				+								
139.	*Stephanodiscus astraea* (EHRBG.) GRUN.					500		1 500	+				
140.	*Surirella biseriata* BRÉB. β—m				+		+			3 750	+	1 250	+
141.	*Surirella biseriata* var. *diminuta* CLEVE—EULER				+								+
142.	*Surirella elegans* EHRBG. β—m												
143.	*Surirella ovata* KÜTZ. β—m						+	1 000					
144.	*Surirella robusta* EHRBG. var. *splendida* EHRBG.) v. HEURCK β—α—m		+				+		+		+		+
145.	*Surirella tenera* GREG. β—α—m										+		+
146.	*Synedra actinastroides* LEMM. β—α—m									20 000	+	40 000	+

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
147.	*Synedra acus* Kütz. o—β—m					500		1 000	+				
148.	*Synedra affinis* Kütz. o—β—m		+		+				+	6 250	+	1 250	+
149.	*Synedra ulna* (Nitzsch) Ehrbg. o—β—m	2 600		1 500	+	6 000	+	9 000	+		+		+
150.	*Synedra ulna var. biceps* (Kütz.) Hust.						+						
151.	*Synedra ulna* var. *biceps* (Kütz.) Hust. v. Heurck β—α—m				+		+						
152.	*Synedra ulna* var. *spathulifera* Grun.										+		
153.	*Thalassiosira fluviatilis* Cleve									10 000	+	8 750	+
	übrige Algen	600		260		5 000		4 500		67 800		69 300	
	sämtliche Algen	12 400		3 040		25 000		44 500		526 250		788 750	
	Zahl der angetroffenen Algentaxone	30		39		40		43		77		74	

DAS MENARCHE-ALTER DER MÄDCHEN VON SÜDUNGARN

von

GY. FARKAS

Anthropologisches Institut der Universität Szeged, Ungarn
(Dir.: Doz. Dr. P. LIPTÁK)

Das Körperwachstum der Kinder wird in den letzten 10—15 Jahren von den ungarischen Anthropologen sehr intensiv untersucht (6). In dieser Arbeit nimmt das Anthropologisches Institut der Universität zu Szeged besonders vom Jahre 1958 teil. In dem erwähnten Jahr hat in Szeged eine grössere Angabensammlung begonnen, deren Ergebnisse bereits veröffentlicht wurden (2). Diese Untersuchung gibt aber nur in einem gegebenen Alter bezüglich der Wachstumverhältnisse der Kinder vom verschiedenem Lebensalter und Geschlecht Auskunft. Die auf solcher Weise gewonnenen Angaben widerspigeln, wie allgemein bekannt, diejenige Gesetzmässigkeiten, die bei einer Untersuchungsserie im Falle des Wachstums zum Vorschein kommen nicht genau. Die Untersuchung nur der Körpermassen gibt besonders in dem Pubertätsalter keine genaue Auskunft über die Veränderungen des Jugendalters. Deshalb wurden bereits im Laufe der Angabensammlung im Jahre 1958 die ersten Monatsblutungen der Mädchen in Betracht genommen. Diese erscheint, wie bekannt, bei der Mädchen in der Pubertät auf einem gewissen Tage und ihre Untersuchung erleichtert die Bestimmung der physiologischen Reife. Ausserdem hat sie auch eine praktische Bedeutung.

Bei der Angabensammlung im Jahre 1958 wurden die Zeitpünkte der ersten Blutung bei allen untersuchten Altersgruppen (2) aufgeschrieben (Tabelle 1.). Im Jahre 1961 war die Möglichkeit vorhanden, eine grössere Sammlung für eine Mediane des ganzen Landes zu gewinnen. Diese Arbeit vollzog sich und die Ergebnisse wurden von einer Arbeitsgruppe in der letzten Zeit bekanntgegeben (1). Im Laufe dieser letzten Angabensammlung wurden nur die Schüler der Grundschule, die die 6—8-te Klasse besuchen laut von den vorherigen Untersuchungen abweichenden Gesichtspünkte gefragt. Die Angaben der Untersuchungen wurden durch eine Probit-Analyse ausgewertet. Die letzte Angabensammlung hat aber nur die Stadt Szeged und ihre unmittelbare Umgebung berührt.

Im Jahre 1962 wurde eine Serienuntersuchung angefangen, die auf vier Jahre geplant ist und zahlreiche Teile von Ungarn berührt. Im Rahmen dieser Untersuchung macht das Institut von Szeged in Szeged, in Pécs und in Budapest systematische, halbjährlich wiederholte Angabensammlungen. Zu derselber Zeit wurden auch unsere Untersuchungen bezüglich der Menarche erweitert und die Menarche-Angaben der Mädchen der Städte in Südungarn zusammengesammelt. Das Ergebnis einer Untersuchung in Orosháza, die mit ethnischen Untersuchungen verbunden ist, wird bald erscheinen (4). Die Auswertung des Musters von Pécs — mit den bisherigen Angaben der Kinder, die in ähnlicher geographischen Zone leben, vergleichend — ist die Aufgabe dieses Aufsatzes.

Tab. 1. Die Verteilung der Angabensammlungen von Südungarn laut Ortschaften und Altersgruppen

Alters gruppe	Szeged 1958/59		Szeged 1961		Umgebung von Szeged 1961		Komitat Csongrád 1961		Orosháza 1963		Pécs 1963		Zusammen			Probit des Prozentes der menstruierenden
	N	Daraus menstr.	N	Daraus menstr.	N	Daraus menstr.	N	Daraus menstr.	N	Daraus menstr.	N	Daraus menstr.	N	Daraus menstr.	%	
11	74	—	—	—	—	—	—	—	—	—	—	—	75	—	—	—
11,5	87	8	108	9	51	6	159	15	19	2	22	3	287	28	9,76	3,70
12	75	10	210	40	109	11	319	51	52	12	126	32	572	105	18,48	4,10
12,5	77	14	244	78	144	31	388	109	71	23	125	56	661	202	30,56	4,19
13	69	29	219	97	135	45	354	142	73	42	136	88	632	301	47,63	4,94
13,5	68	39	268	171	144	78	412	249	73	49	152	107	705	444	62,98	5,33
14	102	81	225	184	178	134	403	318	63	46	176	150	744	595	79,97	5,84
14,5	144	133	146	132	99	76	245	208	36	32	139	125	564	498	88,30	6,19
15	123	118	39	34	29	28	68	62	7	6	20	19	218	205	94,04	6,55
15,5	96	94	10	10	10	9	20	19	9	9	6	6	131	128	97,71	6,99
16	94	94	4	4	3	3	7	7	2	1	1	1	104	103	99,04	7,33
16,5	102	101	—	—	—	—	—	—	—	—	1	1	103	102	99,03	7,33
17	71	71	—	—	—	—	—	—	—	—	2	2	73	73	100,00	—
17,5	62	62	—	—	—	—	—	—	—	—	—	—	62	62	100,00	—
18	40	40	—	—	—	—	—	—	—	—	—	—	40	40	100,00	—
18,5	6	6	—	—	—	—	—	—	—	—	1	1	7	7	100,00	—
19	4	4	—	—	—	—	—	—	—	—	—	—	4	4	100,00	—
?	—	—	—	—	—	—	—	—	10	7	4	3	14	10	71,43	5,57
Zusammen	1294	904	1473	759	902	421	2375	1180	416	229	911	594	4996	2907	58,19	—

Tab. 2.

Die Verteilung des Untersuchungsmaterials von Pécs laut Schultypen und Altersgruppen

Altersgruppe	Koeduzierte Klassen			Reine Mädchenklassen			Zusammen gefragt		
	N	Daraus menstr.	%	N	Daraus menstr.	%	N	Daraus menstr.	%
11,5	19	3	15,8	—	—	—	22	3	13,63
12	115	29	25,2	—	—	—	126	32	25,39
12,5	110	50	45,5	3	1	33,3	125	56	44,80
13	101	69	68,3	26	14	53,9	136	88	64,71
13,5	103	74	71,9	35	25	71,4	152	107	70,39
14	107	91	85,1	52	44	84,6	176	150	85,23
14,5	72	66	91,7	56	48	85,7	139	125	89,92
15	15	14	93,3	4	4	100,0	20	19	95,00
15,5	3	3	100,0	1	1	100,0	6	6	100,00
16	1	1	100,0	—	—	—	1	1	100,00
16,5	1	1	100,0	—	—	—	1	1	100,00
17	1	1	100,0	1	1	100,0	2	2	100,00
17,5	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
18,5	—	—	—	1	1	100,0	1	1	100,00
?	4	3	75,0	—	—	—	4	3	75,00
Zusammen	652	405	62,1	179	139	77,7	911	594	65,20

Material und Methode

In diesem Aufsatz möchten wir vor allem die Angaben der Untersuchungen von Pécs bekanntgeben, weil die Auskünfte bezüglich der in anderen Ortschaften gesammelten Angaben, die in den Tabellen vorkommen, in unseren früheren Publikationen zu finden sind (1, 2, 3, 4).

In Pécs haben wir Angaben über die 6—8-te Klassen besuchenden Kinder zwischen dem 2-ten März und dem 30-ten April, vorwiegend zwischen dem 18-ten und dem 30-ten April gesammelt. Auf den Angabensammlungsbogen waren die folgenden Fragen zu finden: Geburtsort und -Zeit, Beruf der Eltern, hat sie schon Monatsblutung gehabt oder nicht, Zeitpunkt der ersten und der ersten periodischen Blutung, Datum der Angabensammlung. Die Ausfüllung der Bogen wurde mit der Hilfe der Lehrerinnen gemacht. Das Material der

koeduzierten und reinen Klassen wurde nach Altersgruppen an der Tabelle Nr. 2 angegeben. Das Material einer Schule, weder in der Gruppe der koeduzierten, noch in der Gruppe der reinen Mädchenklassen kommt nicht vor, es wurde nur in dem vereinigten Ergebnis in Betracht genommen, wir haben nähmlich bis zum Beginn der Bearbeitung der Angaben keine genaue Auskunft bezüglich der Koedukation bekommen. Wir haben die Altersgruppen mit halbjährlicher Genauigkeit (vollendetes Halbjahr $\pm$ 3 Monate) bestimmt.

Die zur Probit-Analyse nötige Angaben sind in der Tabelle Nr. 3 bekanntgegeben. In der Tabelle Nr. 4 haben wir das Prozent der menstruirenden laut Untersuchungsorte gruppiert. Wir möchten hier bemerken, dass mit der Hilfe der Tabelle die Möglichkeit vorhanden sei, die Angaben der Kinder, die unter verschiedenen geographischen und klimatischen Verhältnissen wohnen, zu vergleichen. In der Tabelle vertritt Szeged die stark industrialisierende, vorher landwirtschaftliche Grossstadt, Orosháza den kleineren Marktflecken, Pécs die industrialisierte Gross-Stadt im Mittelgebirge und Salgótarján die industrialisierte Kleinstadt des Mittelgebirges.

Tab. 3. Die wichtigsten Angaben der regressiven Gleichung der Lebensalter- und Menarche Probit. (Mädchen von Pécs).

Altersgruppe x	Zusammen n	Daraus menstr.		Probit des Prozentes der menstruierenden
		Fälle r	% p	
11,5	22	3	13,6	3,90
12	126	32	25,4	4,34
12,5	125	56	44,8	4,87
13	136	88	64,7	5,38
13,5	152	107	70,4	5,54
14	176	150	85,2	6,05
14,5	139	125	89,9	6,28
15	20	19	95,0	6,65
Zusammen:	896	580	64,7	—

Im Laufe der Auswertung — ähnlich zu unseren früheren Untersuchungen — haben wir auch die Verteilung der monatlichen Erscheinung der ersten Blutung beobachtet, (Tabelle 5). Auch bei dem Material von Pécs haben wir das Menarche-Alter der Mädchen ausgerechnet, d. h. das genaue Lebensalter, wo die Blutung zum ersten mal erscheint. Natürlich war dies nur im Fälle möglich, wo das gefragte Mädchen den genauen Zeitpunkt der ersten Blutung sagen konnte. Bezüglich des Zusammenhanges zwischen dem Menarche-Alter und der monatliche Erscheinung der Blutung gibt die Tabelle Nr. 6 Auskunft. Die Menarche-Lebensaltersgruppen haben wir halbjährlich zusammengebracht und in jedem Untersuchungsort die Häufigkeit der Erscheinung der Blutung in einzelnen Gruppen bestimmt (Tabelle 7). Die Tabelle Nr. 8 weist auf den

Zusammenhang des Geburtsmonates und des Menarche-Monates der Mädchen hin. In der Tabelle Nr. 9 können wir die Korrelation der Menarche-Jahreszeiten (= die Jahreszeit, wo das Mädchen geboren ist, bzw. wo bei ihr die Menarche aufgetreten ist beobachten).

In den Tabellen teilen wir unter dem Schlagwort „Komitat Csongrád" die Angaben, die in der Stadt Szeged und in ihrer Umgebung im Jahre 1961 gesammelt wurden, beisammen mit. Diese Werte wurden bei dem vereinigten Ergebnis nicht in Betracht genommen, da sie in den Angaben von Szeged und von der Umgebung von Szeged schon einmal ausgeschrieben worden sind.

Untersuchungsergebnisse

In den Ortschaften von Südungarn wurden 4996 Mädchen gefragt, bis zum Zeitpunkt der Angabensammlung ist die Blutung bei 2907 erschienen. Das macht 58,19% der gefragten aus. Bei der Serie von Pécs haben wir dagegen einen mit 14,7% höheren Wert gefunden. Bei dieser letzten kann die Menarche Mediane der koeduzierten Klassen auf 12,75 Jahr, die der reinen Mädchen-Klassen auf 12,85 Jahr geschätzt werden. Es gibt keinen grösseren Unterschied zwischen den beiden, durch Probit-Analyse gewonnenen Werten, was von der Feststellung des früheren Materials von Ungarn unterstützt wird (1), d. h. dass der Schultyp auf diese Erscheinung keinen Einfluss habe. Wir müssen aber bemerken, dass der Muster von Pécs in dieser Hinsicht nicht ganz einwandfrei sei, weil das Untersuchungsmaterial der gefragten Kinder der verschiedenen Schultyp von einander bedeutend abweicht. (Fällennummer der Lebensgruppen usw.).

Eine grössere Bedeutung hat die Tabelle Nr. 4, woraus festgestellt werden kann, dass bei den 11,5 jährigen das Auftreten der Blutung im grössten Prozent bei dem Material von Pécs und Salgótarján zu finden sei, dagegen die in den Städten der ungarischen Tiefebene lebenden Kinder in ähnlichem Lebensalter eine mindere Häufigkeit aufweisen. Das Muster von Pécs fällt auch in jener Hinsicht auf, dass bis den 11,5—14 Jahren in allen Altersgruppen das Auftreten der Menarche in höherem Prozent wahrzunehmen ist.

Das monatliche Auftreten der Blutung ist im Fälle der einzelnen Ortschaften ähnlich. Eine gemeinsame Züge ist, dass die grösste Häufigkeit bei jedem einzelnen Muster im Monat Januar erscheint. Die Häufigkeit des Monats Januar ist in Pécs minder, als die des Südungarns. Die grösste Zahl der Erscheinung haben wir bei den Untersuchungen in der Stadt Szeged 1961 beobachtet. Im Fälle der Städte der grossen ungarischen Tiefebene fällt die zweigrösste Häufigkeit auf die Wintermonate (Dezember bzw. Februar). Die Mädchen von Pécs weichen auch in dieser Hinsicht ab, nähmlich kommt bei ihnen die grösste Häufigkeit mit der Ausnahme von Januar im Vergleich mit den anderen Monaten in August vor. Bei allen Angaben von Südungarn ist August der Monat, der die zweitgrösste Häufigkeit aufweist, aber bloss mit 0,6% in die Richtung der höheren Werte abweichend.

Im Fälle der Mädchen von Pécs — ebenso wie bei den Schülern anderer Städte — fällt das Auftreten der Blutung meistens zwischen die 11 3/4 und 13 1/2 Lebensjahre. Der Muster von Pécs steht — die Verteilung betrachtend

— zum Ergebnis der Untersuchungen von Szeged vom Jahre 1961 am nächsten (Tabelle 7).

Wenn wir die Geburst- und Menarche-Monate in Betracht nehmen, fällt auf, dass im Fälle der Mädchen von Pécs, unabhängig vom Geburstmonat die erste Blutung im allgemeinen im Monat Januar erscheint — im Vergleich mit den anderen Monaten —. Die geringste Wahrscheinlichkeit zur Meldung der ersten Blutung zeigt sich im Monat Mai und Oktober.

Auf Grund des ganzen Untersuchungsmusters von Südungarn kann festgestellt werden, dass die erste Blutung der Mädchen unabhängig davon, in welcher Jahreszeit sie geboren sind, in erster Linie im Winter erscheint und zwar 2719 Fällen in 1015.

Zur Schätzung der Menarche-Mediane haben wir im Fälle des Musters von Pécs dreierlei Möglichkeiten. Falls wir die untere Altersgruppe betrachten, kann die Mediane auf 12,65 Jahr geschätzt werden (Abb. 1). Wenn wir die Gerade auf solcher Weise streichen, dass sie die meisten Altersgruppen berühre, zeigt sich die Mediane 12,90. Hier haben wir auch die Möglichkeit, dass wir die Gerade auf Grund der Probit der 12 und 14 jährigen streichen — in diesem Fälle betrachten wir 715 aus 911 Fällen — so kann die Mediane im Wert von 12,80 bestimmt werden. Wir halten diese letztere für wahrscheinlichere. Betrachten wir aber irgendwelche, fällt auf, dass die Werte kleinere sind als die Mediane, die wir im Fälle irgendwelches von uns in Südungarn untersuchten Materials gefunden haben. Am meisten Nähert sich dieser Wert zu den Medianen von Budapest, Salgótarján, Komitat Nógrád und Kaposvár (1,6). Wir sehen also, dass die Mädchen von Pécs in gewisser Hinsicht eine abweichende Fälle in Südungarn vertreten.

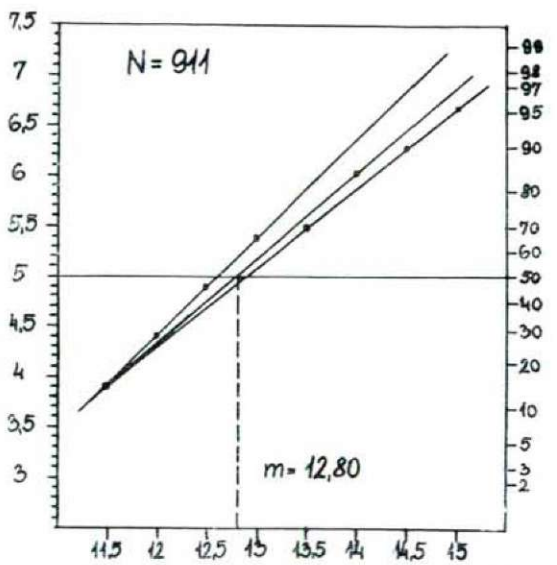

Abb. 1. Die Bestimmung der Mediane des Menarche-Alters, die Darstellung der Zusammenhanges zwischen Lebensalter und Menarche mit Probit-Methode. — Die Mädchen von Pécs.

Tab. 4.

Das Prozent der menstruierenden laut Untersuchungsorten und Altersgruppen

Altersgruppe	Das Prozent der menstruierenden nach Untersuchungsorte							
	Szeged 1958/59	Szeged 1961	Umgebung von Szeged 1961	Komitat Csongrád 1961	Orosháza 1963	Pécs 1963	Salgótarján 1960	Umgebung von Salgótarján 1960
11,5	9,2	8,3	11,8	9,4	10,5	13,6	15,6	10,0
12	13,3	19,0	10,1	16,0	23,0	25,4	17,9	23,8
12,5	18,2	32,0	21,5	28,1	32,4	44,8	32,9	50,0
13	42,0	44,3	33,3	40,1	57,5	64,7	55,1	63,6
13,5	57,4	63,8	54,2	60,4	67,1	70,4	70,0	35,3
14	79,4	81,8	75,3	78,9	73,0	85,2	78,9	83,3
14,5	92,4	90,4	76,8	84,9	88,9	89,9	80,0	80,0
15	95,9	87,2	96,6	91,2	85,7	95,0	100,0	—
15,5	97,9	100,0	90,0	95,0	100,0	—	100,0	—
N	841	1469	899	2368	403	902	371	92

Auf Grund des Musters des ganzen Südungarns kann die Mediane 13,05 Lebensjahr geschätzt werden (Abb. 2). Grösser als diese ist das Menarche-Alter der Mädchen von Szeged, von der Umgebung der Stadt und von Orosháza, die der Mädchen von Pécs vertritt einen kleineren Wert. Das Menarche-Alter der Mädchen von Südungarn ist kleiner, als die Landes-Mediane (6).

Der Muster von Pécs zeigt also ein Ergebnis, welches von den klimatischen Regeln zu erwarten ist und folgt nicht die Gesetzmässigkeiten, die auf das ganze Land verallgemeinert sind, laut derer das Alter der Menarche von Norden nach Süden, und von Ost nach West wächtst (1). Wir bemerken im Zusammenhang dieser Feststellung, dass sie auf Grund der Muster von kleineren Fällennummern festgestellt wurden. Es wird einen Zweifel gehegt, ob die Verminderung des Menarche Zeitalters wirklich von Norden nach Süden sich vollziehe (selbstverständlich betrifft diese Feststellung vor allem Ungarn und nicht die ganze Welt!). Diesen Zweifel stärkt zum Beispiel Prokopec, in dem er auf Grund seiner Angaben, verfertigt 1953—58, veröffentlicht 1961 in Prag, die Mediane auf 12 Jahre und 8 Monate schätzt (6). Auch die schon erwähnten Angaben von Budapest (6) bestimmen die Mediane unter 13 Jahre. Wir finden also bei den Kindern von Prag, Budapest und Pécs im wesentlichen ähnliche Werte. Die Mediane von West-Europa sind auch vom höheren Werte (6). Unserer Meinung nach, worauf es bereits hingewiesen wurde (4), sollen wir hier vor allem eine klimatische Wirkung annehmen. Das wird im Fälle unseres Musters von Pécs auch davon unterstützt, dass das Klima

Tab. 5.

Die monatliche Verteilung des Auftretens der Menarche laut Untersuchungsorten

Zeitpunkt der ersten Blutung	Szeged 1958/59		Szeged 1961		Umgebung von Szeged 1961		Komitat Csongrád 1961		Orosháza 1963		Pécs 1963		Zusammen	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Januar	125	16,2	150	20,5	69	16,6	219	19,1	41	18,1	95	16,2	480	17,6
Februar	51	6,6	50	6,8	61	14,7	111	9,7	23	10,1	56	9,6	241	8,8
März	42	5,5	40	5,5	41	9,9	81	7,1	15	6,6	43	7,4	181	6,6
April	36	4,7	29	4,0	15	3,6	44	3,8	10	4,4	51	8,7	141	5,2
Mai	56	7,3	37	5,1	14	3,4	51	4,4	9	4,0	32	5,5	148	5,4
Juni	54	7,0	55	7,5	27	6,5	82	7,1	22	9,7	38	6,5	196	7,2
Juli	60	7,8	45	6,2	24	5,8	69	6,0	9	4,0	37	6,3	175	6,4
August	98	12,7	79	10,8	33	7,9	112	9,8	20	8,8	80	13,7	310	11,4
September	49	6,4	61	8,3	23	5,5	84	7,3	15	6,6	38	6,5	186	6,8
Oktober	64	8,3	44	6,0	18	4,3	62	5,4	14	6,2	31	5,3	171	6,3
November	52	6,8	62	8,5	39	9,4	101	8,8	17	7,5	36	6,2	206	7,5
Dezember	84	10,9	80	10,9	52	12,5	132	11,5	32	14,1	48	8,2	296	10,8
Zusammen	171	—	732	—	416	—	1148	—	227	—	585	—	2731	—

im Gebirge Mecsek, wo auch die Stadt Pécs liegt, in gewisser Hinsicht vom Klima der untersuchten Städte der Tiefebene abweicht. Das kann auch in den Tier und Pflanzen-Coenosen ausgezeigt werden und es scheint so, dass es auch auf die untersuchte Erscheinung gültig sei.

Tab. 6. Zusammenhang zwischen dem Menarche-Alter der Mädchen und dem ersten Monat der Auftretens der ersten Blutung (Mädchen von Pécs).

Der Monat wo die Blutung erschien		Das Lebensalter der Mädchen wo die Menarche erschien				
		—11½	11¾—12½	12¾—13½	13¾—14½	14¾—
Januar		9	35	34	12	1
Februar		6	25	15	4	—
März		6	13	14	4	—
April		6	17	17	3	2
Mai		3	9	10	1	—
Juni		7	10	12	1	1
Juli		5	12	11	1	—
August		14	26	30	8	—
September		5	10	10	6	—
Oktober		2	9	10	3	—
November		3	11	12	4	—
Dezember		6	11	18	6	—
Zusammen	N	72	188	193	53	4
	%	14,1	36,9	37,8	10,4	0,8
		510				

Tab. 7.

Die Verteilung der Angaben der Untersuchungen von Südungarn laut des Menarche-Lebensalters

Ort und Zeit der Untersuchung	—11½	11¾—12½	12¾—13½	13¾—14½	14¾—
	Menarche-Lebensalter				
Szeged 1958 59	8,64%	29,52%	38,96%	19,08%	3,81%
Szeged 1961	15,07%	37,76%	36,26%	10,29%	0,59%
Umgebung von Szeged 1961	8,08%	25,54%	41,91%	19,44%	1,01%
Komitat Csongrád 1961	12,47%	34,70%	38,36%	13,69%	0,75%
Orosháza 1963	17,51%	35,02%	34,10%	12,44%	0,92%
Pécs 1963	14,11%	36,86%	37,84%	10,39%	0,78%

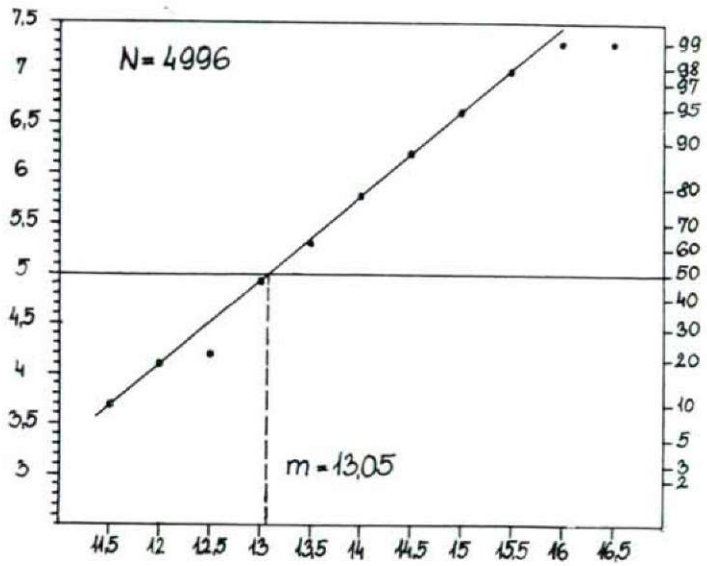

Abb. 2. Die Bestimmung der Mediane des Menarche-Alters, die Darstellung des Zusammenhanges zwischen Lebensalter und Menarche mit Probit-Methode. — Die Mädchen von Südungarn.

Tab. 8.

Der Zusammenhang zwischen dem Geburtsmonate und dem Menarche-Monate bei den Mädchen von Pécs

Geburtsmonat			Menarche-Monat												Zusammen	
			Frühling			Sommer			Herbst			Winter				
			III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	I.	II.		
	Frühling	III.	8	8	2	2	5	10	2	1	4	4	10	9	65	
		IV.	6	6	4	—	1	8	3	2	—	4	10	6	50	160
		V.	4	4	2	—	3	10	4	2	1	4	7	4	45	
	Sommer	VI.	3	1	3	7	2	2	—	4	1	4	9	5	41	
		VII.	3	4	1	2	7	7	1	1	1	7	12	5	51	142
		VIII.	6	3	3	4	1	9	5	3	4	3	5	4	50	
	Herbst	IX.	2	5	—	4	3	6	4	4	5	6	11	6	56	
		X.	4	7	1	3	5	9	5	3	9	3	12	3	64	159
		XI.	2	1	6	3	1	4	5	—	3	5	5	4	39	
	Winter	XII.	4	4	3	5	1	8	5	3	3	4	5	4	49	
		I.	1	4	2	3	4	4	2	4	1	3	5	2	35	117
		II.	1	4	2	3	4	3	4	2	1	1	4	4	33	
Zusammen			44	51	29	36	37	80	40	29	33	48	95	56		578
			124			153			102			199				

Tab. 9.

Der Zusammenhang zwischen der Geburtsjahreszeit und der Menarche-Jahreszeit bei den Mädchen von Südungarn laut Untersuchungsorten

Menarche-Jahreszeit		Frühling (III.—V.)				Sommer (VI.—VIII.)				Herbst (IX.—XI.)				Winter (XII.—II.)				Zusammen
Geburts-Jahreszeit		Frühling	Sommer	Herbst	Winter	Frühling	Sommer	Herbst	Winter	Frühling	Sommer	Herbst	Winter	Frühling	Sommer	Herbst	Winter	
Ort und Zeit der Untersuchung	I. Szeged 1958/59	52	21	32	29	60	54	45	53	33	46	50	36	66	50	67	77	771
	II. Szeged 1961	32	21	31	22	45	37	53	44	43	41	50	33	59	69	76	76	732
	III. Umgebung von Szeged 1961	21	21	12	16	18	24	25	17	17	20	21	22	47	46	43	46	416
	IV. Komitat Csongrád 1961	53	42	43	38	63	61	78	61	60	61	71	55	106	115	119	122	1148
	V. Orosháza 1963	10	5	10	9	12	18	13	7	14	7	14	9	22	29	14	29	222
	VI. Pécs 1963	44	27	28	25	39	41	38	35	19	20	38	25	58	54	55	32	578
I+II+III+V+VI		159	95	113	101	174	174	174	156	126	134	173	125	252	248	255	260	2719

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